HAND-BOOK

OF

PHYSIOLOGY.

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BY

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PREFACE TO THE NINTH EDITION.

At the present time, the average length of life of new physiological facts may be reckoned, so it is said, at about three years; and there is sufficient truth in the sarcasm to make the work of selection of facts for a Student's Handbook of Physiology a somewhat difficult matter. It is, indeed, impossible to do more than pick out those which seem, from various analogies, most likely to have a long term of existence, or to take their place ultimately among established truths. So much, however, I have endeavoured to do,—remembering that the present work is intended only as a student's guide to those parts of the science of Physiology which are either incontrovertible, or at least fairly established; it makes no pretensions of being either a complete treatise or a work of reference.

In the preparation of the present edition I have received great assistance from my friend Mr. Harold Schofield, more particularly in the histological portions of the work—the chapters on the Structural Composition of the Human Body, on the Elementary Tissues, and a portion of the chapter on Generation and Development having been in great part re-written by him. In other parts of the work he has also rendered me much help; and many of the new illustrations are contributed by him from original drawings of microscopic specimens prepared by himself.

Chapter II. is reprinted, almost verbatim, from an article

which I contributed in 1867 to St. Bartholomew's Hospital Reports.

Many of the chapters have been in part re-cast, or re-written. Indeed, the present edition contains comparatively little of the original work of Dr. Kirkes; but I have preserved, as far as possible, the general plan and arrangement of the book, as being, on the whole, best adapted for the purpose for which it was written.

For convenience of reference I have inserted, as an Appendix, Tables of various Anatomical Weights and Measures, of the Specific Gravities of some Tissues and Fluids, of the Composition of certain Foods, and of the Classification of the Animal Kingdom.

To Dr. Klein I am indebted for permission to copy several histological drawings in the 'Handbook for the Physiological Laboratory' and elsewhere; and to Mr. W. Pye for original drawings to illustrate the subjects of Muscle, the Kidney, and the Retina. I am desirous of expressing my obligations also to Dr. Allen Thomson for several illustrations, taken from the anatomical drawings which he has contributed to the later editions of Quain's Anatomy; and to Dr. John Williams for contributing to that part of the section on Generation which relates to "the Structure of the Mucous Membrane of the Uterus, and its periodical changes."

About 150 additional illustrations appear in the present edition. They have been drawn by Mr. Godart and Mr. Collings, and engraved by Mr. J. D. Cooper.

W. MORRANT BAKER.

26, Wimpole Street, London,
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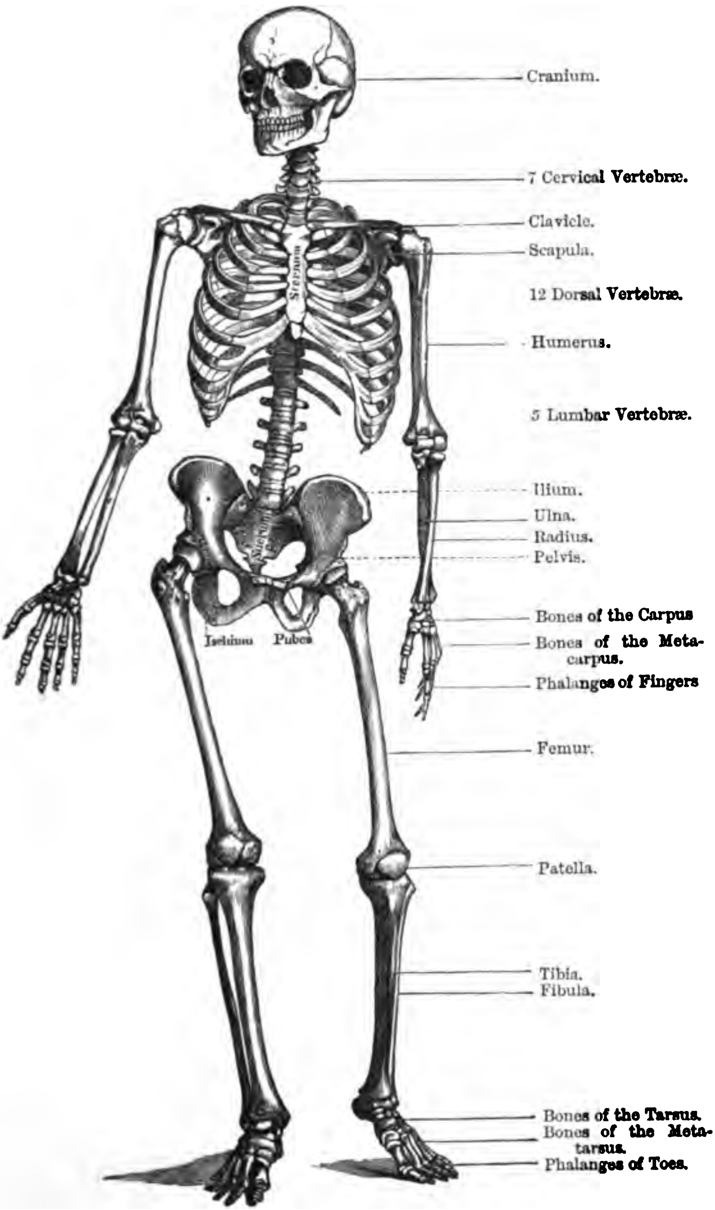

THE SKELETON (AFTER HOLDEN).

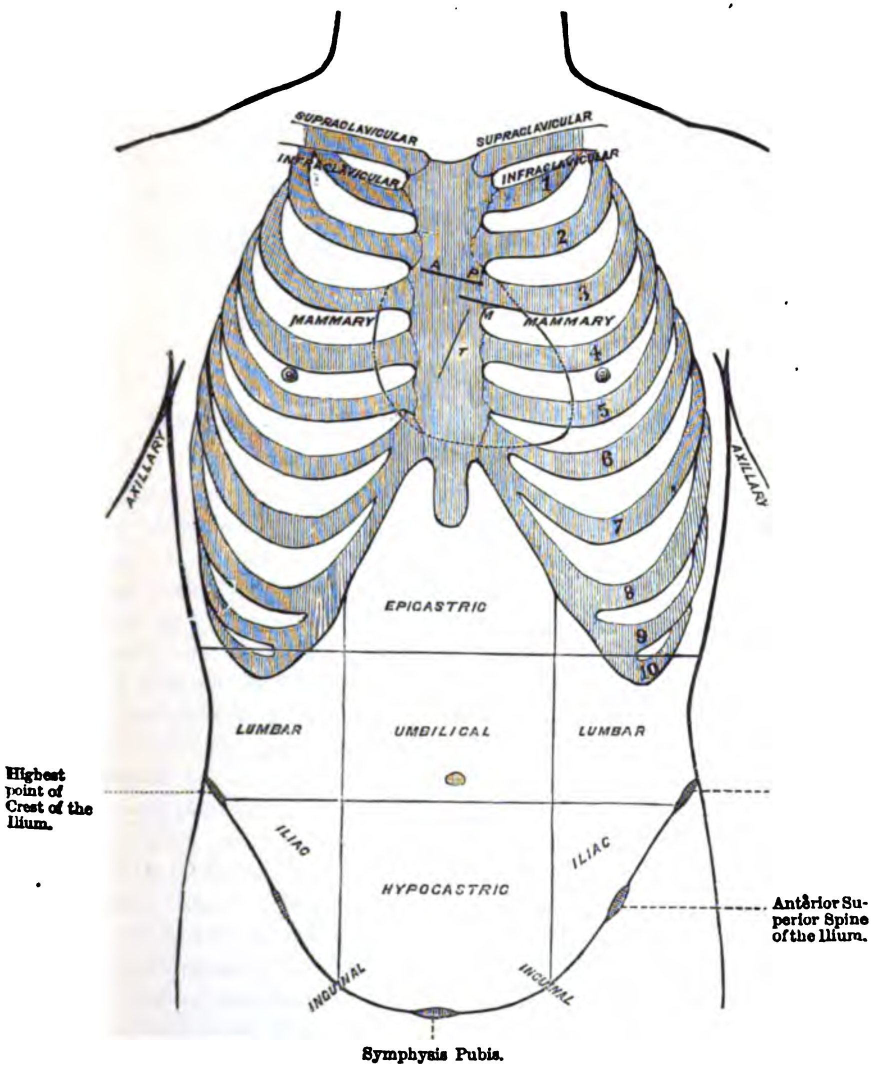

DIAGRAM OF THORACIC AND ABDOMINAL REGIONS.

The Cardiac region is shown by a dotted outline.

A. Site of Aortic Valve. *P.* Pulmonary Valve.
M. Mitral Valve. *T.* Tricuspid Valve.

HANDBOOK OF PHYSIOLOGY.

CHAPTER I.

THE GENERAL AND DISTINCTIVE CHARACTERS OF LIVING BEINGS.

HUMAN PHYSIOLOGY is the science which treats of the life of man—of the way in which he lives, and moves, and has his being. It teaches how man is begotten and born; how he attains maturity; and how he dies.

Having, then, man as the object of its study, it is unnecessary to speak here of the laws of life in general, and the means by which they are carried out, further than is requisite for the more clear understanding of those of the life of man in particular. Yet it would be impossible to understand rightly the working of a complex machine without some knowledge of its motive power in the simplest form; and it may be well to see first what are the so-called essentials of life—those, namely, which are manifested by all living beings alike, by the lowest vegetable and the highest animal, before proceeding to the consideration of the structure and endowments of the organs and tissue belonging to man.

The essentials of life are these,—birth, growth and development, decline and death.

The term, *birth*, when employed in this general sense of one of the conditions essential to life, without reference to any particular kind of living being, may be taken to mean, separation from a parent, with a greater or less power of independent life.

Taken thus, the term, although not defining any particular stage in development, serves well enough for the expression of

the fact, to which no exception has yet been proved to exist, that the capacity for life in all living beings is got by inheritance.

Growth, or inherent power of increasing in size, although essential to our idea of life, is not confined to living beings. A crystal of common salt, or of any other substance, if placed under appropriate conditions for obtaining fresh material, will grow in a fashion as definitely characteristic and as easily to be foretold as that of a living creature. It is, therefore, necessary to explain the distinctions which exist in this respect between living and lifeless structures; for the manner of growth in the two cases is widely different.

First, the growth of a crystal, to use the same example as before, takes place merely by additions to its outside; the new matter is laid on particle by particle, and layer by layer, and, when once laid on, it remains unchanged. The growth is here said to be *superficial*. In a living structure, on the other hand, as, for example, a brain or a muscle, where growth occurs, it is by addition of new matter, not to the surface only, but throughout every part of the mass; the growth is not superficial but *interstitial*. In the second place, all living structures are subject to constant decay; and life consists not, as once supposed, in the power of preventing this never-ceasing decay, but rather in making up for the loss attendant on it by never-ceasing repair. Thus, a man's body is not composed of exactly the same particles day after day, although to all intents he remains the same individual. Almost every part is changed by degrees; but the change is so gradual, and the renewal of that which is lost so exact, that no difference may be noticed, except at long intervals of time. A lifeless structure, as a crystal, is subject to no such laws; neither decay nor repair is a necessary condition of its existence. That which is true of structures which never had to do with life is true also with respect to those which, though they are formed by living parts, are not themselves alive. Thus, an oyster-shell is formed by the living animal which it encloses, but it is as lifeless as any other mass of inorganic matter; and in accordance with this circumstance its growth takes place not *interstitially*, but layer by layer, and it is not

subject to the constant decay and reconstruction which belong to the living. The hair and nails are examples of the same fact.

Thirdly,—in connection with the growth of lifeless masses there is no alteration in the chemical constitution of the material which is taken up and added to the previously existing mass. For example, when a crystal of common salt grows on being placed in a fluid which contains the same material, the properties of the salt are not changed by being taken out of the liquid by the crystal and added to its surface in a solid form. But the case is essentially different in living beings, both animal and vegetable. A plant, like a crystal, can only grow when fresh material is presented to it; and this is absorbed by its leaves and roots; and animals for the same purpose of getting new matter for growth and nutrition, take food into their stomachs. But in both these cases the materials are much altered before they are finally *assimilated* by the structures they are destined to nourish.

Fourthly. The growth of all living things has a definite limit, and the law which governs this limitation of increase in size is so invariable that we should be as much astonished to find an individual plant or animal without limit as to growth as without limit to life.

Development is as constant an accompaniment of life as growth. The term is used to indicate that change to which, before maturity, all living parts are constantly subject, and by which they are made more and more capable of performing their several functions. For example, a full-grown man is not merely a magnified child; his tissues and organs have not only grown, or increased in size, they have also *developed*, or become better in quality.

No very accurate limit can be drawn between the end of development and the beginning of decline; and the two processes may be often seen together in the same individual. But after a time all parts alike share in the tendency to degeneration, and this is at length succeeded by death.

It has been already said that the essential features of life are the same in all living things; in other words, in the members

of both the animal and vegetable kingdoms. It may be well to notice briefly the distinctions which exist between the members of these two kingdoms. It may seem, indeed, a strange notion that it is possible to confound vegetables with animals, but it is true with respect to the lowest of them, in which but little is manifested beyond the essentials of life, which are the same in both.

I. Perhaps the most essential distinction is the presence or absence of power to live upon *inorganic* material. By means of their green colouring matter, *chlorophyll*—a substance almost exclusively confined to the vegetable kingdom, plants are capable of decomposing the carbonic acid, ammonia and water, which they absorb by their leaves and roots, and thus utilizing them as food. The result of this chemical action, which occurs only under the influence of light, is, so far as the carbonic acid is concerned, the fixation of carbon in the plant structures, and the exhalation of oxygen. Animals are incapable of thus using inorganic matter, and never exhale oxygen, as a product of decomposition.

The power of living upon organic as well as inorganic matter is less decisive of an animal nature; inasmuch as fungi and some other plants derive their nourishment in part from the former source.

II. There is, commonly, a marked difference in general chemical composition between vegetables and animals, even in their lowest forms; for while the former consists mainly of *cellulose*, a substance closely allied to starch and containing carbon, hydrogen, and oxygen only, the latter are composed in great part of the three elements just named, together with a fourth, nitrogen; the chief proximate principles formed from these being identical, or nearly so, with *albumen*. It must not be supposed, however, that either of these typical compounds alone, with its allies, is confined to one kingdom of nature. Nitrogenous compounds are freely produced in vegetable structures, although they form a very much smaller proportion of the whole organism than cellulose or starch. And while the presence of the latter in animals is much more rare than is that

of the former in vegetables, there are many animals in which traces of it may be discovered, and some, the Ascidians, in which it is found in considerable quantity.

III. Inherent power of movement is a quality which we so commonly consider an essential indication of animal nature, that it is difficult at first to conceive it existing in any other. The capability of simple motion is now known, however, to exist in so many vegetable forms, that it can no longer be held as an essential distinction between them and animals, and, ceases to be a mark by which the one can be distinguished from the other. Thus the zoospores of many of the Cryptogamia exhibit ciliary or amœboid movements (p. 46) of a like kind to those seen in animalcules; and even among the higher orders of plants, many exhibit such motion, either at regular times, or on the application of external irritation, as might lead one, were this fact taken by itself, to regard them as sentient beings. Inherent power of movement, then, although especially characteristic of animal nature, is, when taken by itself, no proof of it.

IV. The presence of a digestive canal is a very general mark by which an animal can be distinguished from a vegetable. But the lowest animals are surrounded by material that they can take as food, as a plant is surrounded by an atmosphere that it can use in like manner. And every part of their body being adapted to absorb and digest, they have no need of a special receptacle for nutrient matter, and accordingly have no digestive canal. This distinction then is not a cardinal one.

It would be tedious as well as unnecessary to enumerate the chief distinctions between the more highly developed animals and vegetables. They are sufficiently apparent. It is necessary to compare, side by side, the lowest members of the two kingdoms, in order to understand rightly how faint are the boundaries between them.

CHAPTER II.*

ON THE RELATION OF LIFE TO OTHER FORCES.

An enumeration of theories concerning the nature of life would be beside the purpose of the present chapter. They are interesting as marks of the way in which various minds have been influenced by the mystery which has always hung about vitality; their destruction is but another warning that any theory we can frame must be considered only a tie for connecting present facts, and one that must yield or break on any addition to the number which it is to bind together.

Before attention had been drawn to the mutual convertibility of the various so-called physical forces—heat, light, electricity, and others—and until it had been shown that these, like the matter through which they act, are limited in amount, and strictly measurable; that a given quantity of one force can produce a certain quantity of another and no more; that a given quantity of combustible material can produce only a given quantity of steam, and this again only so much motive power; it was natural that men's minds should be satisfied with the thought that vital force was some peculiar innate power, unlimited by matter, and altogether independent of structure and organisation. The comparison of life to a flame is probably as early as any thought about life at all. And so long as light and heat were thought to be inherent qualities of certain material which perished utterly in their production, it is not strange that life also should have been reckoned some strange spirit, pent up in the germ, expending itself in growth and development, and finally declining and perishing with the body which it had inhabited.

With the recognition, however, of a distinct correlation between the physical forces, came as a natural consequence a revolution of the commonly accepted theories concerning life also.

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* This chapter is a reprint, with some verbal alterations, of an essay contributed by the Editor to *St. Bartholomew's Hospital Reports*, 1867.

The dictum, so long accepted, that life was essentially independent of physical force began to be questioned.

As it is well-nigh impossible to give a definition of life that shall be short, comprehensive, and intelligible, it will be best, perhaps, to take its chief manifestations, and see how far these seem to be dependent on other forces in nature, and how connected with them.

Life manifests itself by birth, growth, development, decline and death; and an idea of life will most naturally arise by taking these events in succession, and studying them individually, and in relation to each other.

When the embryo in a seed awakes from that state, neither life nor death, which is called dormant vitality, and, bursting its envelopes, begins to grow up and develope, it may be said that there is a birth. And so, when the chick escapes from the egg, and when any living form is, as the phrase goes, brought into the world. In each case, however, birth is not the beginning of life, but only the continuation of it under different conditions. To understand the beginning of life in any individual, whether plant or animal, existence must be traced somewhat further back, and in this way an idea gained concerning the nature of the germ, the development of which is to issue in birth.

The germ may be defined as that portion of the parent which is set apart with power to grow up into the likeness of the being from which it has been derived.

The manner in which the germ is separated from the parent does not here concern us. It belongs to the special subject of generation. Neither need we consider apart from others those modes of propagation, as fission and gemmation, which differ more apparently than really from the ordinary process typified in the formation of the seed or ovum. In every case alike, a new individual plant or animal is a portion of its parent; it may be a mere outgrowth or bud, which, if separated, can maintain an independent existence; it may be not an outgrowth but simply a portion of the parent's structure, which has been naturally or artificially cut off, as in the spontaneous or artificial cleaving of

a polype; it may be the embryo of a seed or ovum, as in those cases in which the process of multiplication of different organs has reached the point of separation of the individual more or less completely into two sexes, the mutual conjugation of a portion of each of which, the sperm-cell and the germ-cell, is necessary for the production of a new being. We are so accustomed to regard the conjugation of the two sexes as necessary for what is called generation, that we are apt to forget that it is only gradually in the upward progress of development of the vegetable and animal kingdoms, that those portions of organised matter which are to produce new beings are allotted to two separate individuals. In the least developed forms of life, almost any part of the body is capable of assuming the characters of a separate individual; and propagation, therefore, occurs by fission or gemmation in some form or other. Then, in beings a little higher in rank, only a special part of the body can become a separate being, and only by conjugation with another special part. Still, there is but one parent; and this hermaphrodite-form of generation is the rule in the vegetable and least developed portion of the animal kingdom. At last, in all animals but the lowest, and in some plants, the portions of organised structure specialised for development after their mutual union into a new individual, are found on two distinct beings, which we call respectively male and female.

The old idea concerning the power of growth resident in the germ of the new being, thus formed in various ways, was expressed by saying that a store of dormant vitality was laid up in it, and that so long as no decomposition ensued, this was capable of manifesting itself and becoming active under the influence of certain external conditions. Thus, the dormant force supposed to be present in the seed or the egg was assumed to be the primary agent in effecting development and growth, and to continue in action during the whole term of life of the living being, animal or vegetable, in which it was said to reside. The influence of external forces—heat, light, and others—was noticed and appreciated; but these were thought to have no other connection with vital force than that in some

way or other they called it into action, and that to some extent it was dependent on them for its continuance. They were not supposed to be correlated with it in any other sense than this.

Now, however, we are obliged to modify considerably our notions and with them our terms of expression, when describing the origin and birth of a new being.

To take, as before, the simplest case—a seed or egg. We must suppose that the heat, which in conjunction with moisture is necessary for the development of those changes which issue in the growth of a new plant or animal, is not simply an agent which so stimulates the dormant vitality in the seed or egg as to make it cause growth, but it is a force, which is itself transformed into chemical and vital power. The embryo in the seed or egg is a part which can transform heat into vital force, this term being a convenient one wherewith to express the power which particular structures possess of growing, developing, and performing other actions which we call vital.* Of course the embryo can grow only by taking up fresh material and incorporating it with its own structure, and therefore it is surrounded in the seed or ovum with matter sufficient for nutrition until it can obtain fresh supplies from without. The absorption of this nutrient matter involves an expenditure of force of some kind or other, inasmuch as it implies the raising of simple to more complicated forms. Hence the necessity for heat or some other power before the embryo can exhibit any sign of life. It would be quite as impossible for the germ to begin life without external force as without a supply of nutrient matter. Without the force wherewith to take it, the matter would be useless. The heat, therefore, which in conjunction with moisture is necessary for the beginning of life, is partly expended as chemical power, which causes certain modifications in the nutrient material surrounding the embryo, e.g., the transformation of starch into sugar in the act of germination; partly, it is

* The term "vital force" is here employed for the sake of brevity. Whether it is strictly admissible will be discussed hereafter.

The general term *force* is used as synonymous with what is now often termed *energy*.

transformed by the germ itself into vital force, whereby the germ is enabled to take up the nutrient material presented to it, and arrange it in forms characteristic of life. Thus the force is expended, and thus life begins—when a particle of organised matter, which has itself been produced by the agency of life, begins to transform external force into vital force, or in other words into a power by which it is enabled to grow and develope. This is the true beginning of life. The time of birth is but a particular period in the process of development at which the germ, having arrived at a fit state for a more independent existence, steps forth into the outer world.

The term 'dormant vitality,' must be taken to mean simply the existence of organized matter with the *capacity* of transforming heat or other force into vital or growing power, when this force is applied to it under proper conditions.

The state of dormant vitality is like that of an empty voltaic battery, or a steam-engine in which the fuel is not yet lighted. In the former case no electric current passes, because no chemical action is going on. There is no transformation into electric force, because there is no chemical force to be transformed. Yet, we do not say, in this instance, that there is a store of electricity laid up in a dormant state in the battery; neither do we say that a store of motion is laid up in the steam-engine. And there is as little reason for saying there is a store of vitality in a dormant seed or ovum.

Next to the beginning of life, we have to consider how far its continuance by growth and development is dependent on external force and to what extent correlated with it.

Mere growth is not a special peculiarity of living beings. A crystal, if placed in a proper solution, will increase in size and preserve its own characteristic outline; and even if it be injured, the flaw can be in part or wholly repaired. The manner of its growth, however, is very different from that of a living being, and the process as it occurs in the latter will be made more evident by a comparison of the two cases. The increase of a crystal takes place simply by the laying of material on the surface only, and is unaccompanied by any interstitial change.

This is, however, but an accidental difference. A much greater one is to be found in the fact that with the growth of a crystal there is no decay at the same time, and proceeding with it side by side. Since there is no life there is no need of death—the one being a condition consequent on the other. During the whole life of a living being, on the other hand, there is unceasing change. At different periods of existence the relation between waste and repair is of course different. In early life the addition is greater than the loss, and so there is growth; the reconstructed part is better than it was before, and so there is development. In the decline of life, on the contrary, the renewal is less than the destruction, and instead of development there is degeneration. But at no time is there perfect rest or stability.

It must not be supposed, therefore, that life consists in the capability of resisting decay. Formerly, when but little or nothing was known about the laws which regulate the existence of living beings, it was reasonable enough to entertain such an idea; and, indeed, life was thought to be, essentially, a mysterious power counteracting that tendency to decay which is so evident when life has departed. Now, we know that so far from life preventing decomposition, it is absolutely dependent upon it for all its manifestations.

The reason of this is very evident. Apart from the doctrine of correlation of force, it is of course plain that tissues which do work must sooner or later wear out if not constantly supplied with nourishment; and the need of a continual supply of food, on the one hand, and, on the other, the constant excretion of matter which, having evidently discharged what was required of it, was fit only to be cast out, taught this fact very plainly. But although, to a certain extent, the dependence of vital power on supplies of matter from without was recognised and appreciated, the true relation between the demand and supply was not until recently thoroughly grasped. The doctrine of the correlation of vital with other forces was not understood.

To make this more plain, it will be well to take an instance of transformation of force more commonly known and appreciated. In the steam-engine a certain amount of force is

exhibited as motion, and the immediate agent in the production of this is steam, which again is the result of a certain expenditure of heat. Thus, heat is in this instance said to be transformed into motion, or, in other language, one—molecular—mode of motion, heat, is made to express itself by another—mechanical—mode, ordinary movement. But the heat which produced the vapour is itself the product of the combustion of fuel, or, in other words, it is the correlated expression of another force—chemical, namely, that affinity of carbon and hydrogen for oxygen which is satisfied in the act of combustion. Again, the production of light and heat by the burning of coal and wood is only the giving out again of that heat and light of the sun which were used in their production. For, as it need scarcely be said, it is only by means of these solar forces that the leaves of plants can decompose carbonic acid, &c., and thereby provide material for the construction of woody tissue. Thus, coal and wood being products of the expenditure of force, must be taken to represent a certain amount of power; and, according to the law of the correlation of forces, must be capable of yielding, in some shape or other, just so much as was exercised in their formation. The amount of force requisite for rending asunder the elements of carbonic acid is exactly that amount which will again be manifested when they clash together again.

The sun, then, really, is the prime agent in the movement of the steam-engine, as it is indeed in the production of nearly all the power manifested on this globe. In this particular instance, speaking roughly, its light and heat are manifested successively as vital and chemical force in the growth of plants, as heat and light again in the burning fuel, and lastly by the piston and wheels of the engine as motive power. We may use the term transformation of force if we will, or say that throughout the cycle of changes there is but once force variously manifesting itself. It matters not, so that we keep clearly in view the notion that all force, so far at least as our present knowledge extends, is but a representative, it may be in the same form or another, of some previous force, and incapable like matter of being created afresh, except by the Creator. Much of our knowledge

on this subject is of course confined to ideas and governed by the words with which we are compelled to express them, rather than to actual things or facts; and probably the term force will soon lose the signification which we now attach to it. What is now known, however, about the relation of one force to another, is not sufficient for the complete destruction of old ideas; and, therefore, in applying the examples of transformation of physical force to the explanation of vital phenomena, we are compelled still to use a vocabulary which was framed for expressing many notions now obsolete.

The dependence of the lowest kind of vital existence on external force, and the manner in which this is used as a means whereby life is manifested, have been incidentally referred to more than once when describing the origin of vegetable tissues. The main functions of the vegetable kingdom are construction, and the perpetuation of the race; and the use which is made of external physical force is more simple than in animals. The transformation indeed which is effected, while much less mysterious than in the latter instance, forms an interesting link between animal and crystalline growth.

The decomposition of carbonic acid or ammonia by the leaves of plants may be compared to that of water by a galvanic current. In both cases a force is applied through a special material medium, and the result is a separation of the elements of which each compound is formed. On the return of the elements to their original state of union, there will be the return also in some form or other of the force which was used to separate them. Vegetable growth, moreover, with which we are now specially concerned, resembles somewhat the increase of unorganised matter. The accidental difference of its being in one case superficial, and in the other interstitial, is but little marked in the process as it occurs in the more permanent parts of vegetable tissues. The layers of lignine are in their arrangement nearly as simple as those of a crystal, and almost or quite as lifeless. After their deposition, moreover, they undergo no further change than that caused by the addition of fresh matter, and hence they are not instances of that ceaseless waste and

repair which have been referred to as so characteristic of the higher forms of living tissue. There is, however, no contradiction here of the axiom, that where there is life there is constant change. Those parts of a vegetable organism in which active life is going on are subject, like the tissues of animals, to constant destruction and renewal. But, in the more permanent parts, life ceases with deposition and construction. Addition of fresh matter may occur, and so may decay also of that which is already laid down, but the two processes are not related to each other, and not, as in living parts, inter-dependent. Hence the change is not a vital one.

The acquirement in growth, moreover, of a definite shape in the case of a tree, is no more admirable or mysterious than the production of a crystal. That chloride of sodium should naturally assume the form of a cube is as inexplicable as that an acorn should grow into an oak, or an ovum into a man. When we learn the cause in the one case, we shall probably in the other also.

There is nothing, therefore, in the products of life's more simple forms that need make us start at the notion of their being the products of only a special transformation of ordinary physical force. And we cannot doubt that the growth and development of animals obey the same general laws that govern the formation of plants. The connecting links between them are too numerous for the acceptance of any other supposition. Both kingdoms alike are expressions of vital force, which is itself but a term for a special transformation of ordinary physical force. The mode of the transformation is, indeed, mysterious, but so is that of heat into light, or of either into mechanical motion or chemical affinity. All forms of life are as absolutely dependent on external physical force as a fire is dependent for its continuance on a supply of fuel; and there is as much reason to be certain that vital force is an expression or representation of the physical forces, especially heat and light, as that these are the correlates of some force or other which has acted or is acting on the substances which, as we say, produce them.

In the tissues of plants, as just said, there is but little change,

except such as is produced by additions of fresh matter. That which is once deposited alters but little; or, if the part be transient and easily perishable, the alteration is only or chiefly one produced by the ordinary process of decay. Little or no force is manifested; or, if it be, it is only the heat of the slow oxidation whereby the structure again returns to inorganic shape. There is no special transformation of force to which the term vital can be applied. With construction the chief end of vegetable existence has been attained, and the tissue formed represents a store of force to be used, but not by the being which laid it up. The labours of the vegetable world are not for itself but for animals. The power laid up by the one is spent by the other. Hence the reason that the constant change, which is so great a character of life, is comparatively but little marked in plants. It is present, but only in living portions of the organism, and in these it is but limited. In a tree the greater part of the tissues may be considered dead; the only change they suffer is that fresh matter is piled on to them. They are not the seat of any transformation of force, and therefore, although their existence is the result of living action, they do not themselves live. Force is, so to speak, laid up in them, but they do not themselves spend it. Those portions of a vegetable organism which are doing active vital work—which are using the sun's light and heat, as a means whereby to prepare building material, are, however, the seat of unceasing change. Their existence as living tissue depends upon this fact—upon their capability of perishing and being renewed.

And this leads to the answer to the question, What is the cause of the constant change which occurs in the living parts of animals and vegetables, which is so invariable an accompaniment of life, that we refuse the title of "living" to parts not attended by it? It is because all manifestations of life are exhibitions of power, and as no power can be originated by us; as, according to the doctrine of correlation of force, all power is but the representative of some previous force in the same or another form, so, for its production, there must be

expenditure and change somewhere or other. For the vital actions of plants the light and heat of the sun are nearly or quite sufficient, and there is no need of expenditure of that store of force which is laid up in themselves; but with animals the case is different. They cannot directly transform the solar forces into vital power, they must seek it elsewhere. The great use of the vegetable kingdom is therefore to store up power in such a form that it can be used by animals; that so, when in the bodies of the latter, vegetable organised material returns to an inorganic condition, it may give out force in such a manner that it can be transformed by animal tissues, and manifested variously by them as vital power.

Hence, then, we must consider the waste and repair attendant on living growth and development as something more than these words, taken by themselves, imply. The waste is the return to a lower from a higher form of matter; and, in the fall, force is manifested. This force, when specially transformed by organised tissues, we call vital. In the repair, force is laid up. The analogy with ordinary transmutations of physical force is perfect. By the expenditure of heat in a particular manner a weight can be raised. By its fall heat is returned. The molecular motion is but the expression in another form of the mechanical. So with life. There is constant renewal and decay, because it is only so that vital activity can take place. The renewal must be something more than replacement, however, as the decay must be more than simple mechanical loss. The idea of life must include both storing up of force, and its transformation in the expenditure.

Hence we must be careful not to confound the mere preservation of individual form under the circumstances of concurrent waste and repair, with the essential nature of vitality.

Life, in its simplest form, has been happily expressed by Mr. Savory as a state of dynamical equilibrium, since one of its most characteristic features is continual decay, yet with maintenance of the individual by equally constant repair. Since, then, in the preservation of the equilibrium there is ceaseless change, it is not static equilibrium but dynamical.

Care must be taken, however, not to accept the term in too strict a sense, and not to confound that which is but a necessary attendant on life with life itself. For, indeed, strictly, there is no preservation of equilibrium during life. Each vital act is an advance towards death. We are accustomed to make use of the terms growth and development in the sense of progress in one direction, and the words decline and decay with an opposite signification, as if, like the ebb of the tide, there were after maturity a reversal of life's current. But, to use an equally old comparison, life is really a journey always in one direction. It is an ascent, more and more gradual as the summit is approached, so gradual that it is impossible to say when development ends and decline begins. But the descent is on the other side. There is no perfect equilibrium, no halting, no turning back.

The term, therefore, must be used with only a limited signification. There is preservation of the individual, yet, although it may seem a paradox, not of the same individual. A man at one period of his life may retain not a particle of the matter of which formerly he was composed. The preservation of a living being during growth and development is more comparable, indeed, to that of a nation, than of an individual as the term is popularly understood. The elements of which it is made up fulfil a certain work the traditions of which were handed down from their predecessors, and then pass away, leaving the same legacy to those that follow them. The individuality is preserved, but, like all things handed down by tradition, its fashion changes, until at last, perhaps, scarce any likeness to the original can be discovered. Or, as it sometimes happens, the alterations by time are so small that we wonder, not at the change, but the want of it. Yet, in both cases alike, the individuality is preserved, not by the same individual elements throughout, but by a succession of them.

Again, concurrent waste and repair do not imply of necessity the existence of life. It is true that living beings are the chief instances of the simultaneous occurrence of these things. But this happens only because the conditions under which the

functions of life are discharged are the principal examples of the necessity for this unceasing and mingled destruction and renewal. They are the chief, but not the only instances of this curious conjunction.

A theoretical case will make this plain. Suppose an instance of some permanent structure, say a marble statue. If we imagine it to be placed under some external conditions by which each particle of its substance should waste and be replaced, yet with maintenance of its original size and shape, we obtain no idea of life. There is waste and renewal, with preservation of the individual form, but no vitality. And the reason is plain. With the waste of a substance like carbonate of calcium whose attractions are satisfied, there would be no evolution of force; and even if there were, no structure is present with the power to transform or manifest anew any power which might be evolved. With the repair, likewise, there would be no storing of force. The part used to make good the loss is not different from that which disappeared. There is therefore neither storing of force, nor its transformation, nor its expenditure; and therefore there is no life.

But real examples of the preservation of an individual substance, under the circumstances of constant loss and renewal, may be found, yet without any semblance in them of life.

Chemistry, perhaps, affords some of the neatest and best examples of this. One, suggested by Mr. Shepard, seems particularly apposite. It is the case of trioxide of nitrogen ($N_2 O_3$) in the preparation of sulphuric acid. The gas from which this acid is obtained is sulphurous acid, and the addition of an equivalent of oxygen is all that is required. Sulphurous acid gas, however, cannot take the necessary oxygen directly from the atmosphere, but it can abstract it from trioxide of nitrogen ($N_2 O_3$), when the two gases are mingled. The trioxide, accordingly, by continually giving up an equivalent of oxygen to an equivalent of sulphurous acid, causes the formation of sulphuric acid, at the same time that it retains its composition by continually absorbing a fresh quantity of oxygen from the atmosphere.

In this instance, then, there is constant waste and repair, yet

without life. And here an objection cannot be raised, as it might be to the preceding example, that both the destruction and repair come from without, and are not dependent on any inherent qualities of the substance with which they have to do. The waste and renewal in the last-named example are strictly dependent on the qualities of the chemical compound which is subject to them. It has but to be placed in appropriate conditions, and destruction and repair will continue indefinitely. Force, too, is manifested, but there is nothing present which can transform it into vital shape, and so there is no life.

Hence, our notion of the constant decay which, together with repair, takes place throughout life, must be not confined to any simply mechanical act. It must include the idea, as before said, of laying up of force, and its expenditure—its transformation too, in the act of being expended.

The growth, then, of an animal or vegetable, implies the expenditure of physical force by organised tissue, as a means whereby fresh matter is added to and incorporated with that already existing. In the case of the plant the force used, transformed, and stored up, is almost entirely derived from external sources; the material used is inorganic. The result is a tissue which is not intended for expenditure by the individual which has accumulated it. The force expended in growth by animals, on the other hand, cannot be obtained directly from without. For them a supply of force is necessary in the shape of food derived directly or indirectly from the vegetable kingdom. Part of this force-containing food is expended as fuel for the production of power; and the latter is used as a means wherewith to elaborate another portion of the food, and incorporate it as animal structure. Unlike vegetable structure, however, animal tissues are the seat of constant change, because their object is not the storing up of power, but its expenditure; so there must be constant waste; and if this happen, then for the continuance of life there must be equally constant repair. But, as before said, in early life the repair surpasses the loss, and so there is growth. The part repaired is better than before the loss, and thus there is development.

The definite limit which has been imposed on the duration of life has been already incidentally referred to. Like birth, growth, and development, it belongs essentially to living beings only. Dead structures and those which have never lived are subject to change and destruction, but decay in them is uncertain in its beginning and continuance. It depends almost entirely on external conditions, and differs altogether from the decline of life. The decline and death of living beings are as definite in their occurrence as growth and development. Like these they may be hastened or stayed, especially in the lower forms of life, by various influences from without; but the putting off of decline must be the putting off also of so much life; and, apart from disease, the reverse is true also. A living being starts on its career with a certain amount of work to do—various infinitely in different individuals, but for each well-defined. In the lowest members of both the animal and vegetable creation the progress of life in any given time seems to depend almost entirely on external circumstances; and at first sight it seems almost as if these lowly formed organisms were but the sport of the surrounding elements. But it is only so in appearance, not in reality. Each act of their life is so much expended of the time and work allotted to them; and if, from absence of those surrounding conditions under which alone life is possible, their vitality is stayed for a time, it again proceeds on the renewal of the necessary conditions, from that point which it had already attained. The amount of life to be manifested by any given individual is the same, whether it take a day or a year for its expenditure. Life may be of course at any moment interrupted altogether by disease and death. But supposing it, in any individual organism, to run its natural course, it will attain but the same goal, whatever be its rate of movement. Decline and death, therefore, are but the natural terminations of life; they form part of the conditions on which vital action begins; they are the end towards which it naturally tends. Death, not by disease or injury, is not so much a violent interruption of the course of life, as the attainment of a distant object which was in view from the commencement.

In the period of decline, as during growth, life consists in continued manifestations of transformed physical force; and there is of necessity the same series of changes by which the individual, though bit by bit perishing, yet by constant renewal retains its entity. The difference, as has been more than once said, is in the comparative extent of the loss and reproduction. In decline there is not perfect replacement of that which is lost. Repair becomes less and less perfect. It does not of necessity happen that there is any decrease of the quantity of material added in the place of that which disappears. But although the quantity may not be lessened, and may indeed absolutely increase, it is not perfect as material for repair, and although there may be no wasting, there is degeneration.

No definite period can be assigned as existing between the end of development and the beginning of decline, and chiefly because the two processes go on side by side in different parts of the same organism. The transition as a whole is therefore too gradual for appreciation. But, after some time, all parts alike share in the tendency to degeneration; until at length, being no longer able to subdue external force to vital shape, they die; and the elements of which they are composed simply employ what remnant of power, in the shape of chemical affinity, is still left in them, as a means whereby they may go back to the inorganic world. Of course the same process happens constantly during life; but in death the place of the departing elements is not taken by others.

Here, then, a sharp boundary line is drawn where one kind of action stops and the other begins; where physical force ceases to be manifested except as physical force, and where no further vital transformation takes place, or can in the body ever do so. For the notion of death must include the idea of impossibility of revival, as a distinction from that state of what is called "dormant vitality," in which, although there is no life, there is capability of living. Hence the explanation of the difference between the effect of appliance of external force in the two cases. Take, for examples, the fertile but not yet living egg, and the barren or dead one. Every application of force to

the one must excite movement in the direction of development; the force, if used at all, is transformed by the germ into vital energy, or the power by which it can gather up and elaborate the materials for nutrition by which it is surrounded. Hence its freedom throughout the brooding time from putrefaction. In the other instance, the appliance of force excites only degeneration; if transformed at all, it is only into chemical force, whereby the progress of destruction is hastened; hence it soon rots. To the one, heat is the signal for development, to the other for decay. By one it is taken up and manifested anew, and in a higher form; to the other it gives the impetus for a still quicker fall.

Life, then, does not stand alone. It is but a special manifestation of transformed force. "But if this be so," it may be said —"if the resemblance of life to other forces be great, are not the differences still greater?"

At the first glance, the distinctions between living organised tissue and inorganic matter seem so great that the difficulty is in finding a likeness. And there is no doubt that these wide differences in both outward configuration and intimate composition have been mainly the causes of the delay in the recognition of the claims of life to a place among other forces. And reasonably enough. For the notion that a plant or an animal can have any kind of relationship in the discharge of its functions to a galvanic battery or a steam engine is sufficiently startling to the most credulous. But so it has been proved to be.

Among the distinctions between living and inorganic matter, that which includes differences in structure and proximate chemical composition has been always reckoned a great one. The very terms organic and inorganic were, until quite recently, almost synonymous with those which implied the influence of life and the want of it. The science of chemistry, however, is a great leveller of artificial distinctions; and many organic substances which, it was supposed, could not be formed without the agency of life are now made directly from inorganic material. The number of organic substances so formed artificially is constantly increasing; and there seems to be no reason for

doubting that all organic substances, even such as albumin, gelatin, and the like, will be ultimately produced without the intermediation of living structure.

The formation of the latter, such an organised structure for instance as a cell or a muscular fibre, is a different thing altogether. There is at present no reason for believing that such will ever be formed by artificial means; and, therefore, among the peculiarities of living force-transforming agents, must be reckoned as a great and essential one, a special intimate structure, apart from mere ultimate or proximate chemical composition, to which there is no close likeness in any artificial apparatus, even the most complicated. This is the real distinction, as regards composition, between a living tissue and an inorganic machine; namely, the difference between the structural arrangement by which force is transformed and manifested anew. The fact that one agent for transforming force is made of albumen or the like, and another of zinc or iron, is a great distinction, but not so essential or fundamental an one as the difference in mechanical structure and arrangement.

In proceeding to consider the difference between what may be called the transformation-products of living tissue, and of an artificial machine, it will be well to take one of the simple cases first—the production of mechanical motion; and especially because it is so common in both.

In one we can trace the transformation. We know, as a fact, that heat produces expansion (steam), and by constructing an apparatus which provides for the application of the expansive power in opposite directions alternately, or by alternating contraction with expansion, we are able to produce motion so as to subserve an infinite variety of purposes. For the continuance of the motion there must be a constant supply of heat, and therefore of fuel.

In the production of mechanical motion by the alternate contractions of muscular fibres we cannot trace the transformation of force at all. We know that the constant supply of force is as necessary in this instance as in the other; and that the food which an animal absorbs is as necessary as the fuel in the

former case, and is analogous with it in function. In what exact relation, however, the latent force in the food stands to the movement in the fibre, we are at present quite ignorant. That in some way or other, however, the transformation occurs, we may feel quite certain.

There is another distinction between the two exhibitions of force which must be noticed. It has been universally believed, almost up to the present time, that in the production of living force the result is obtained by an exactly corresponding waste of the tissue which produces it; that, for instance, the power of each contraction of a muscle is the exact equivalent of the force produced by the more or less complete descent of so much muscular substance to inorganic, or less complex organic shape; in other words,—that the immediate fuel which an animal requires for the production of force is derived from its own substance; and that the food taken must first be appropriated by, and enter into the very formation of living tissue before its latent force can be transformed and manifested as vital power. And here, it might be said, is a great distinction between a living structure and a simply mechanical arrangement such as that which has been used for comparison; the fuel which is analogous to the food of a plant or animal does not, as in the case of the latter, first form part of the machine which transforms its latent energy into another variety of power.

We are not, at present, in a position to deny that this is a real and great distinction between the two cases; but modern investigations in more than one direction lead to the belief that we must hesitate before allowing such a difference to be an universal or essential one. The experiments referred to seem conclusive in regard to the production of muscular power in greater amount than can be accounted for by the products of muscular waste excreted; and it may be said with justice, that there is no intrinsic improbability in the supposed occurrence of transformation of force, apart from equivalent nutrition and subsequent destruction of the transforming agent. Argument from analogy, indeed, would be in favour of the more recent theory as the likelier of the two.

Whatever may be the result of investigations concerning the relation of waste of living tissue to the production of power, there can be no doubt, of course, that the changes in any part which is the seat of vital action must be considerable, not only from what may be called "wear and tear," but, also, on account of the great instability of all organised structures. Between such waste as this, however, and that of an inorganic machine there is only the difference in degree, arising necessarily from diversity of structure, of elemental arrangement, and so forth. But the repair in the two cases is different. The capability of reconstruction in a living body is an inherent quality like that which causes growth in a special shape or to a certain degree. At present we know nothing really of its nature, and we are therefore compelled to express the fact of its existence by such terms as "inherent power," "individual endowment," and the like, and wait for more facts which may ultimately explain it. This special quality is not indeed one of living things alone. The repair of a crystal in definite shape is equally an "individual endowment," or "inherent peculiarity," of the nature of which we are equally ignorant. In the case, however, of an inorganic machine there is nothing of the sort, not even as in a crystal. Faults of structure must be repaired by some means entirely from without. And as our notion of a living being, say a horse, would be entirely altered if flaws in his composition were repaired by external means only; so, in like manner, would our idea of the nature of a steam engine be completely changed had it the power of absorbing and using part of its fuel as matter wherewith to repair any ordinary injury it might sustain.

It is this ignorance of the nature of such an act as reconstruction which causes it to be said, with apparent reason, that so long as the term "vital force" is used, so long do we beg the question at issue—What is the nature of life? A little consideration, however, will show that the justice of this criticism depends on the manner in which the word "vital" is used. If by it we intend to express an idea of something which arises in a totally different manner from other forces—something which,

we know not how, depends on a special innate quality of living beings, and owns no dependence on ordinary physical force, but is simply stimulated by it, and has no correlation with it—then. indeed, it would be just to say that the whole matter is merely shelved if we retain the term "vital force."

But if a distinct correlation be recognised between ordinary physical force and that which in various shapes is manifested by living beings; if it be granted that every act—say, for example, of a brain or muscle—is the exactly correlated expression of a certain quantity of force latent in the food with which an animal is nourished; and that the force produced either in the shape of thought or movement is but the transformed expression of external force, and can no more originate in a living organ without supplies of force from without, than can that organ itself be formed or nourished without supplies of matter;—if these facts be recognised, then the term used in speaking of the powers exercised by a living being is not of very much consequence. We have as much right to use the term "vital" as the words galvanic and chemical. All alike are but the expressions of our ignorance concerning the nature of that power of which all that we call "forces" are various manifestations. The difference is in the apparatus by which the force is transformed.

It is with this meaning that, for the present, the term 'vital force' may still be retained when we wish shortly to name that combination of energies which we call life. For, exult as we may at the discovery of the transformation of physical force into vital action, we must acknowledge not only that, with the exception of some slight details, we are utterly ignorant of the process by which the transformation is effected; but, as well, that the result is in many ways altogether different from that of any other force with which we are acquainted.

It is impossible to define in what respects, exactly, vital force differs from any other. For while some of its manifestations are identical with ordinary physical force, others have no parallel whatsoever. And it is this mixed nature which has hitherto baffled all attempts to define life, and, like a Will-o'-the-wisp, has led us floundering on through one definition

after another only to escape our grasp and show our impotence to seize it.

In examining, therefore, the distinctions between the products of transformations by a living and by an inorganic machine, we have first to recognise the fact, that while in some cases the difference is so faint as to be nearly or quite imperceptible, in others there seems not a trace of resemblance to be discovered.

In discussing the nature of life's manifestations—birth, growth, development, and decline—the differences which exist between them and other processes more or less resembling them, but not dependent on life, have been already briefly considered and need not be here repeated. It may be well, however, to sum up very shortly the particulars in which life as a manifestation of force differs from all others.

The mere acquirement of a certain shape by growth is not a peculiarity of life. But the power of developing into so composite a mass even as a vegetable cell is a property possessed by an organised being only. In the increase of inorganic matter there is no development. The minutest crystal of any given salt has exactly the same shape and intimate structure as the largest. With the growth there is no development. There is increase of size with retention of the original shape, but nothing more. And if we consider the matter a little we shall see a reason for this. In all force-transformers, whether living or inorganic, with but few exceptions—and these are, probably, apparent only—something more is required than homogeneity of structure. There seems to be a need for some mutual dependence of one part or another, some distinction of qualities, which cannot happen when all portions are exactly alike. And here lies the resemblance between a living being and an artificial machine. Both are developments, and depend for their power of transforming force on that mutual relation of the several parts of their structure which we call organisation. But here, also, lies a great difference. The development of a living being is due to an inherent tendency to assume a certain form; about which tendency we know absolutely nothing. We recognise the fact, and that is all. The development of an inorganic machine—say an electrical apparatus

—is not due to any inherent or individual property. It is the result of a power entirely from without; and we know exactly how to construct it.

Here, then, again, we recognise the compound nature of a living being. In structure it is altogether different from a crystal —in inherent capacity of growth into definite shape it resembles it. Again, in the fact of its organisation it resembles a machine made by man: in capacity of growth it entirely differs from it. In regard, therefore, to structure, growth, and development, it has combined in itself qualities which in all other things are more or less completely separated.

That modification of ordinary growth and development called generation, which consists in the natural production and separation of a portion of organised structure, with power itself to transform force so as therewith to build up an organism like the being from which it was thrown off, is another distinctive peculiarity of a living being. We know of nothing like it in the inorganic world. And the distinction is the greater because it is the fulfilment of a purpose, towards which life is evidently, from its very beginning, constantly tending. It is as natural a destiny to separate parts which shall form independent beings as it is to develop a limb. Hence it is another instance of that carrying out of certain projects, from the very beginning in view, which is so characteristic of things living and of no other.

It is especially in the discharge of what are called the animal functions that we see vital force most strangely manifested. It is true that one of the actions included in this term—namely, mechanical movement—although one of the most striking, is by no means a distinctive one. For it must be remembered that one of the commonest transformations of physical force with which we are acquainted is that of heat into mechanical motion, and that this may be effected by an apparatus having itself nothing whatever to do with life. The peculiarity of the manifestation in an animal or vegetable is that of the organ by which it is effected, and the manner in which the transformation takes place, not in the ultimate result. The mere fact of an animal's possessing capability of movement is not more wonderful than

the possession of a similar property by a steam engine. In both cases alike, the motion is the correlative expression of force latent in the food and fuel respectively; but in one case we can trace the transformation in the arrangement of parts, in the other we cannot.

The consideration of the products of the transformation of force effected by the nervous system would lead far beyond the limits of the present chapter. But although the relation of mind to matter is so little known that it is impossible to speak with any freedom concerning such correlative expressions of physical force as thought and other nerve-products, still it cannot be doubted that they are as much the results of transformation of force as the mechanical motion caused by the contraction of a muscle. But here the mystery reaches its climax. We neither know how the change is effected, nor the nature of the product, nor its analogies with other forces. It is therefore better, for the present, to confess our ignorance, than, with the knowledge which we have lately gained, to build up rash theories, serving only to cause that confusion which is worse than error.

It may be said, with perfect justice, that even if the foregoing conclusions be accepted, namely, that all manifestations of force by living beings are correlative expressions of ordinary physical force, still the argument is based on the assumption of the existence of the apparatus which we call living organised matter, with power not only to use external force for its own use in growth, development, and other vital manifestations, but for that modification of these powers which consists in the separation of a part that shall grow up into the likeness of its parent, and thus continue the race. We are therefore, it may be added, as far as ever from any explanation of the origin of life. This is of course quite true. The object of the present chapter, however, is only to deal with the now commonly accepted views regarding the relations of life, as it now exists, to other forces. The manner of creation of the various kinds of organised matter, and the source of those its qualities which from our ignorance we call inherent, are different questions altogether.

To say that of necessity the power to form living organised matter will never be vouchsafed to us, that it is only a mere

materialist who would believe in such a possibility, seems almost as absurd as the statement that such inquiries lead of necessity to the denial of any higher power than that which in various forms is manifested as "force," on this small portion of the universe. It is almost as absurd, but not quite. For, surely, he who recognises the doctrine of the mutual convertibility of all forces, vital and physical, who believes in their unity and imperishableness, should be the last to doubt the existence of an all-powerful Being, of whose will they are but the various correlative expressions; from whom they all come; to whom they return.

CHAPTER III.

CHEMICAL COMPOSITION OF THE HUMAN BODY.

THE following *Elementary Substances* may be obtained by chemical analysis from the human body: Oxygen, Hydrogen, Nitrogen, Carbon, Sulphur, Phosphorus, Silicon, Chlorine, Fluorine, Potassium, Sodium, Calcium, Magnesium, Iron, and, probably as accidental constituents, Lithium, Manganesium, Aluminium, Copper, and Lead. Thus of the sixty-three or more elements of which all known matter is composed, more than one fourth are present in the human body.

The following table represents their relative proportion.—(Marshall).

Oxygen	72·0
Carbon	13·5
Hydrogen	9·1
Nitrogen	2·5
Calcium	1·3
Phosphorus	1·15
Sulphur	·1476
Sodium	·1
Chlorine	·085
Fluorine	·08
Potassium	·026
Iron	·01
Magnesium	·0012
Silicon	·0002
	100·

Only three elements, and in very minute amount, are present in the body uncombined with others. These are Oxygen, Nitrogen, and Hydrogen: oxygen in small amount, in the blood, the greater part, however, of this gas being chemically combined with hæmoglobin (see Blood); nitrogen, in the blood, and other fluids of the body; and hydrogen as well as oxygen and nitrogen, in the intestinal canal.

The same elements exist, of course, abundantly in various states of combination.

The compounds formed by union of the elements in various proportions are termed *proximate* principles; while the latter are classified as the *organic* and the *inorganic* proximate principles.

The term *organic* was once applied exclusively to those substances which were thought to be beyond the compass of synthetical chemistry and to be formed only by *organised* or living beings, animal or vegetable; these being called organised, inasmuch as they are characterised by the possession of different parts called organs. But with advancing knowledge, both distinctions have disappeared; and while the title of living organism is applied to numbers of living things, having no trace of organs in the strict sense of the term, the term organic has long ceased to be applied to substances formed only by living tissues. In other words, substances, once thought to be formed only by living tissues, are still termed organic, although they can be now made in the laboratory: as, for example, urea, oxalic, and tartaric acids, &c.

Although a large number of so-called organic compounds have long ceased to be peculiar in being formed only by living tissues, the terms organic and inorganic are still commonly used to denote distinct classes of chemical substances; and the classification of the matters of which the human body is composed into organic and inorganic is convenient, and will be here employed.

No very accurate distinction can be drawn between organic and inorganic substances, but there are certain peculiarities belonging to the former which may be here briefly noted.

1. Organic compounds are composed of a larger number of *Elements* than are present in the more common kinds of inorganic matter. Thus, albumin, the most abundant substance of this class, in the more highly organised tissues of animals, is composed of five elements,—carbon, hydrogen, oxygen, nitrogen, and sulphur. The most abundant inorganic substance, water, has but two elements, hydrogen and oxygen.

2. Not only are a large number of elements usually combined

in an organic compound, but a large number of *atoms* of each element are united to form a molecule of the compound. In carbonate of ammonium, an example among inorganic substances, there are one atom of carbon, three of oxygen, two of nitrogen, and eight of hydrogen. But in a molecule of albumin, there are of the same elements, respectively, 72, 22, 18, and 112 atoms. And, together with this union of large numbers of atoms in an organic compound, it is further observable, that these numbers stand in no simple arithmetical relation one to another, as do the numbers of the atoms of an inorganic compound.

With these peculiarities in the chemical composition of organic bodies we may connect two other consequent facts; first, the large number of different compounds that are formed out of comparatively few elements; secondly, their great proneness to decomposition. For it is a general rule, that the greater the number of equivalents or atoms of an element that enter into the formation of a molecule of a compound, the less is the stability of that compound. Thus, for example, among the various oxides of lead and other metals, the least stable in composition are those in which each equivalent has the largest number of equivalents of oxygen. So, water, composed of one equivalent of oxygen and two of hydrogen, is not decomposed by any slight force; but peroxide of hydrogen, which has two equivalents of oxygen to two of hydrogen, is a very unstable compound.

The instability, on this ground, belonging to organic compounds, is, in those which are most abundant in the highly organised tissues of animals, augmented, 1st, by their containing nitrogen, which, among all the elements, may be called the least decided in its affinities, and that which maintains with least tenacity its combinations with other elements; and, 2ndly, by the quantity of water which, in their natural state, is combined with them, and the presence of which furnishes a most favourable condition for the decomposition of nitrogenous compounds. Such, indeed, is the instability of animal compounds, arising from these several peculiarities in their constitution, that, in dead and moist animal matter, no more is requisite for the occurrence of decomposition than the presence of atmospheric air

and a moderate temperature; conditions so commonly present, that the decomposition of dead animal bodies appears to be, and is generally called, spontaneous. The modes of such decomposition vary according to the nature of the original compound, the temperature, the access of oxygen, the presence of microscopic organisms, and other circumstances, and constitute the several processes of decay and putrefaction; in the results of which processes the only general rule seems to be, that the several elements of the original compound finally unite to form those substances, whose composition is, under the circumstances, most stable.

The *Organic* compounds existing in the human body may be arranged in two classes, namely, the *Non-Nitrogenous*, and the *Nitrogenous* principles.

Non-Nitrogenous Organic Principles.

The non-nitrogenous principles are comprised in the following classes:—1. Fats and oils. 2. Amyloids. 3. Certain acids.

I. *Fats and Oils.*—(Olein $C_{57} H_{104} O_6$, Stearin $C_{57} H_{110} O_6$, Palmitin $C_{51} H_{98} O_6$). The chief example of this group found in the body is the oil or fatty matter which, enclosed in minute cells, forms the essential part of adipose or fatty tissue, (p. 75) and which is present in greater or less amount in many other tissues and fluids. It consists of a mixture of saponifiable fats,—*stearin*, *palmitin*, and *olein*; the mixture forming a clear yellow oil, of which different specimens congeal at from 45° to 35° F. Thus, in the living body, the fat is in a liquid state, the solidity of adipose tissue being due to the microscopic cells in which the liquid oil is contained and the connective tissue, blood-vessels, &c., in the meshes of which the fat cells are held (p. 76).

The fatty matter of the body is chiefly derived from the fat in the food, which is absorbed, in a manner to be hereafter considered, from the intestinal canal. But it is also indirectly derived in part from other constituents of the food—both amyloids and albuminous principles, in the course of the chemical changes which they undergo in the system.

The uses of adipose tissue will be referred to in a later chapter (p. 77).

From its never-failing presence wherever active cell-growth is proceeding, it may be inferred that fatty matter is of great importance in the processes of growth and development; and that it is of not less importance to healthy nutrition at all times may be gathered from its wide distribution in the solids and fluids of the body. Like other combustible matters, fat scarcely appears in any of the excretions. Its force-producing properties are utilised within the system by direct and indirect combustion; and its elements leave the body in the form of carbonic acid and water.

Cholesterin ($C_{26}\ H_{44}\ O$), a non-saponifiable fat which melts at 293° F., and is, therefore, always solid at the natural temperature of the body, may be obtained in small quantity from blood, bile, and nervous matter. It occurs abundantly in many biliary calculi; the pure white crystalline specimens of these concretions being formed of it almost exclusively. Minute rhomboidal scale-like crystals of it are also often found in morbid secretions, as in cysts, the puriform matter of softening and ulcerating tumours, &c. It is soluble in ether and boiling alcohol; but alkalies do not change it.

Cholesterin is generally regarded rather as a product of chemical change, which is destined for rapid excretion, than a proper constituent part of the body, like the saponifiable fats just referred to; the nervous tissues being especially the site of its production, and the liver the organ by which it is separated from the blood, and cast into the intestine. Dr. Flint believes that another non-saponifiable fat, *stercorin*, which he has discovered in the fæces, is but cholesterin, somewhat modified in chemical constitution, in its passage through the bowel. About ten grains are excreted daily.

Excretin, another non-saponifiable fat, was discovered as a constituent of fæces, by Dr. Marcet.

II. *Amyloids.*—Under this head are included both starch and sugar. These substances, like the fats, contain carbon, hydrogen, and oxygen; but the last named element is present in much larger relative amount, the hydrogen and oxygen being in the proportion to form water.

The following varieties of these substances are found in health in the body.

(*a*) *Glycogen* ($C_6 H_{10} O_5$).—This substance, which is identical in composition with starch, and like it, readily converted into sugar by ferments, is found in many embryonic tissues and in all new formations where active cell-growth is proceeding. It is present also in the placenta. After birth it is found almost exclusively in the liver and muscles.

Glycogen is formed chiefly from the saccharine matters of the food; but although its amount is much increased when the diet largely consists of starch and sugar, these are not its only source. It is still formed when the diet is flesh only, by the decomposition, probably, of albumin into glycogen and urea.

The destination of glycogen will be considered in a subsequent chapter. (See Liver).

(*b*) *Glucose* or *grape-sugar* ($C_6 H_{12} O_6 + H_2 O$) is found in minute quantities in the blood and liver, and occasionally in other parts of the body. It is derived directly from the starches and sugars in the food, or from the glycogen which has been formed in the body from these or other matters. However formed, it is in health quickly burnt off in the blood by union with oxygen, and thus helps in the maintenance of the body's temperature. Like other amyloids it is one source whence fat is derived.

(*c*) *Lactose*, or *sugar of milk* ($C_{12} H_{22} O_{11} + H_2 O$), is formed in large quantity when the mammary glands are in a condition of physiological activity,—human milk containing 5 or 6 per cent. of it. Like other sugars it is a valuable nutritive material, and hence is only discharged from the body when required for the maintenance of the offspring. The same remark is applicable to the other organic nutrient constituents of the milk, albumin and saponifiable fats, which, if we except what is present in the secretions of the generative organs, are discharged from the body only under the same conditions and in the same secretion.

(*d*) *Inosite* ($C_6 H_{12} O_6 + 2 H_2 O$), a variety of sugar, identical in composition with glucose, but differing in some of its properties, is found constantly in small amount in muscle, and occasionally in other tissues. Its origin and uses, in the economy are, presumably, similar to those of glycogen.

III. *Non-Nitrogenous Organic Acids*.—Very few of these acids

exist in a free state in the body, and deserve enumeration among the proximate principles; almost all being in a state of combination, as in the case of ordinary fat, which is a chemical compound of fatty acids with glycerine.

Lactic acid is found in the gastric juice, and in muscle.

Formic, acetic, propionic, butyric, and *caproic* acids occur more or less combined with bases in the sweat. Butyric acid is also found in the contents of the large intestine.

Nitrogenous Organic Principles.

The class of nitrogenous proximate principles embraces a large number of chemical compounds of various constitution and degree of complexity which contain nitrogen in addition to carbon, hydrogen, and oxygen; while some of the most complex contain a minute quantity also of sulphur, and, in one or two instances, of phosphorus.

They may be conveniently, though very roughly, classified as follows:—I. Proteids or albuminoids. II. Gelatinous substances. III. Ferments. IV. Colouring matters. V. Various substances which cannot be included under the previous heads.

I. *Proteids* or *Albuminoids.*

Under this head are included albumin, globulin, myosin, fibrin, casein, syntonin.

A very large proportion of the nitrogenous matters found in the body is formed by the albuminoids; one or more of them entering as essential parts into the formation of all living tissues. In the lymph, chyle, and blood, they also exist abundantly. Their atomic formula is not at present known. The following is the per-centage composition of albumin, which may be taken as the type of the group.

Carbon	53·5
Hydrogen	7·0
Nitrogen	15·5
Oxygen	22·0
Sulphur	1·6
Phosphorus	·4
	100·0

The *albuminoids* are colloid substances, and, in all the forms in which they habitually occur, are combined with phosphate of calcium, chloride of sodium, and other mineral substances, and a greater or less amount of fatty matter and water. They are derived directly from the albuminous constituents of food, and are probably not formed afresh within the body.

The manner in which, as food, they are acted on by the gastric and other digestive fluids, in order to be made fit for absorption into the blood, will be described in the chapter on Digestion. The greater part or all of the other nitrogenous substances in the body are derived directly or indirectly from the albuminoids, which are the subject of continual chemical change; and from the re-arrangement of some of their elements are also produced, it is now believed, a part of the fatty and amyloid constituents.

(a) *Albumin* is present abundantly in the blood and lymph, and in most of the tissues of the body.

(b) *Globulin* and its several modifications, exist largely in the blood and in many of the tissues.

(c) *Myosin*, which is closely allied to globulin, is the substance which spontaneously coagulates, after death, in the juice of muscles.

(d) *Fibrin* is readily obtained, in a somewhat impure state, as a soft, yet tough, elastic, and opaque white, stringy substance, by washing a clot of blood in water, until all its colour has disappeared. It is almost identical in composition with albumin,—the only difference being that fibrin contains 1.5 per cent. more oxygen. Mr. A. H. Smee has, indeed, apparently converted albumin into fibrin by exposing a solution to the prolonged influence of oxygen.

Fibrin is contained in the blood, and, to a less extent, in lymph and chyle. It does not exist as fibrin in the body, but is formed, in the act of coagulation, by the union of two albuminoids termed respectively *fibrinoplastin* and *fibrinogen* (p. 105). The special distinctive character of fibrin is its spontaneous formation by coagulation in fluids which contain these two substances.

(e) *Casein*, an important constituent of milk, and found also in minute amount in the blood and some other parts of the body, is a chemical combination of potash with albumin. It is coagulated by most acids.

A familiar example of such coagulation is afforded by cheese, which is made by precipitating the casein of milk by rennet (calf's stomach).

(f) *Syntonin*, which much resembles fibrin, has been chiefly observed as a product of the action of dilute acids on myosin.

(g) *Mucin* is found in mucus; also in synovia, the vitreous humour, and the umbilical cord. It differs in composition from albumin in not containing sulphur.

II. *Gelatinous Substances.*

Gelatinous substances can be extracted in large quantity from the connective tissues by boiling in water; the solution remaining liquid while it is hot, and becoming solid and jelly-like on cooling.

The composition of gelatin, the type of this group, is as follows:—

Carbon	50·16
Hydrogen	6·6
Nitrogen	18·3
Oxygen	24·8
Sulphur	·14

(a) *Gelatin* can be readily extracted from fibrous connective tissue and from bone by long boiling in water. The solution solidifies, as a jelly, on cooling to about 60° F., even when only one per cent. of gelatin is present. Although insoluble in cold water, gelatin swells enormously when immersed in it; and a mass of gelatin thus swollen is readily liquefied by heat.

(b) *Chondrin* is a gelatinous substance obtained from cartilage. It agrees with gelatin in most of its characters.

(c) *Elastin* is obtained, by long boiling, from yellow elastic tissue. It contains no sulphur, and differs in many other respects from both gelatin and chondrin.

(d) *Keratin* can be extracted from the epidermis and its appendages—hair, nails, &c.

III. *Ferments.*

Certain nitrogenous substances called *ferments* are found in the various secretions of the alimentary canal, namely, the saliva, the gastric and the intestinal juice, the pancreatic juice, and the bile. Their function is to act on various articles of food in such a manner as to fit them for solution and absorption into the blood. Thus *ptyalin* is the ferment of the saliva, by which starchy ingredients of the food are converted into glucose; *pepsin* that of the gastric juice, which changes albuminous ingredients into a soluble dialysable substance called *peptone*. These and other ferments will be considered further in the chapter on Digestion, with the anatomy and physiology of the glands by which they are formed.

IV. *Colouring Matters.*

Of the colouring matters contained in the human body, that of the blood, *hæmoglobin*, is the most important; and, probably, all the others are derived directly or indirectly from it.

Colouring matters are also present in the bile and urine; and in some of the tissues, especially the skin, the eyeball, and other sense-organs.

So far as may be necessary, the colouring matters will be further considered with the tissues and fluids in which they are present (see sections treating of Blood, Bile, Urine, etc.).

V. *Nitrogenous substances not included under the previous heads.*

There are several substances which, apparently, form an essential part of the tissues in which they are found, but which do not belong to any of the preceding classes. Such are *cerebrin* and *lecithin*, and the compound formed by their union,—*protagon*, which enters largely into the composition of nerve-tissue,—*myelin*, *cerebric acid*, and others. Most of these contain phosphorus, in addition to carbon, hydrogen, nitrogen, and oxygen.

Besides—other substances are formed, chiefly by decomposition of nitrogenous materials of the food and of the tissues, which must be reckoned rather as temporary constituents than essential component parts of the body; although from the continual change, which is a necessary condition of life, they are always to be found in greater or less amount. Examples of these are *urea*, *uric* and *hippuric* acids, *creatin*, *creatinin*, *leucin*, *tyrosin*, and many others.

Such are the chief organic substances of which the human body is composed. It must not be supposed, however, that they exist naturally in a state approaching that of chemical purity. All the fluids and tissues of the body consist of mixtures of several of these principles, together with saline matters. Thus, a piece of muscular flesh would yield fibrin, albumin, gelatin, fatty matters, salts of sodium, potassium, calcium, magnesium, iron, and other substances, such as creatin, which are products of chemical decomposition, and, though constant, are not essential constituents of the tissue. This mixture of substances may be explained in some measure by the existence of many different structures or tissues in the muscles; the gelatin may be referred

principally to the connective tissue between the fibres, the fatty matter to the adipose tissue in the same position, and part of the albumin to the blood, and the fluid by which the tissue is kept moist. But, beyond these general statements, little can be said of the mode in which the chemical compounds are united to form an organised structure; or of how, in any organic body, the several incidental substances are combined with those which are essential.

Inorganic Principles.

The inorganic proximate principles of the human body are numerous. They are derived, for the most part, directly from food and drink, and pass through the system unaltered. Some are, however, decomposed on their way, as chloride of sodium, of which only four-fifths of the quantity ingested are excreted in the same form; and some are newly formed within the body,—as for example, a part of the sulphates and carbonates, and some of the water.

Much of the inorganic saline matter found in the body is a necessary constituent of its structure,—as necessary in its way as albumin or any other organic principle; another part is important in regulating or modifying various physical processes, as absorption, solution, and the like; while a part must be reckoned only as matter, which is, so to speak, accidentally present, whether derived from the food or the tissues, and which will, at the first opportunity, be excreted from the body.

The inorganic gaseous matters found in the body are *oxygen*, *hydrogen*, *nitrogen*, *carburetted* and *sulphuretted hydrogen*, and *carbonic acid*. The first three have been referred to (p. 31). Carburetted and sulphuretted hydrogen are found in the intestinal canal. Carbonic acid is present in the blood and other fluids, and is excreted in large quantities by the lungs, and in very minute amount by the skin. It will be specially considered in the chapter on Respiration.

Water, the most abundant of the proximate principles, forms a large proportion,—more than two-thirds, of the weight of the whole body.

Its relative amount in some of the principal solids and fluids of the body is shown in the following table (quoted by Dalton, from Robin and Verdeil's table, compiled from various authors) :—

QUANTITY OF WATER IN 1000 PARTS.

Teeth	100	Bile	880
Bones	130	Milk	887
Cartilage	550	Pancreatic juice	900
Muscles	750	Urine	936
Ligaments	768	Lymph	960
Brain	789	Gastric juice	975
Blood	795	Perspiration	986
Synovia	805	Saliva	995

The importance of water as a constituent of the animal body may be assumed from the preceding table, and is shown in a still more striking manner by its withdrawal. If any tissue,—as muscle, cartilage, or tendon be subjected to heat sufficient to drive off the greater part of its water, all its characteristic physical properties are destroyed; and what was previously soft, elastic, and flexible, becomes hard, and brittle, and horny, so as to be scarcely recognisable.

In all the fluids of the body—blood, lymph, &c., water acts the part of a general solvent, and by its means alone circulation of nutrient matter is possible. It is the medium also in which all fluid and solid aliments are dissolved before absorption, as well as the means by which all, except gaseous, excretory products are removed. All the various processes of secretion, transudation, and nutrition, depend of necessity on its presence for their performance.

The greater part, by far, of the water present in the body is taken into it as such from without, in the food and drink. A small amount, however, is the result of the chemical union of hydrogen with oxygen in the blood and tissues. The total amount taken into the body every day is about 4½ lbs.; while an uncertain quantity (perhaps ½ to ¾ lb.) is formed by chemical action within it.—(Dalton).

The loss of water from the body is intimately connected with excretion from the lungs, skin, and kidneys, and, to a less extent, from the alimentary canal. The loss from these various organs may be thus apportioned (quoted by Dalton from various observers):—

From the Alimentary Canal (fæces)	4	per cent.
,, Lungs	20	,,
,, Skin (perspiration)	30	,,
,, Kidneys (urine)	46	,,
	100	

The *chlorides of sodium* and *potassium* are present in nearly all parts of the body. The former seems to be especially necessary, judging from the instinctive craving for it on the part of animals in whose food it is deficient, and from the diseased condition which is consequent on its withdrawal. In the blood, the quantity of chloride of sodium is greater than that of all its other saline ingredients taken together. In the muscles, on the other hand, the quantity of chloride of sodium is less than that of the chloride of potassium.

Fluoride of calcium, in minute amount, is present in the bones and teeth, and traces have been found in the blood and some other fluids.

The *phosphates* of *calcium, potassium, sodium*, and *magnesium*, are found in nearly every tissue and fluid. In some tissues—the bones and teeth—the phosphate of calcium exists in very large amount and is the principal source of that hardness of texture, on which the proper performance of their functions so much depends. The phosphate of calcium is intimately incorporated with the organic basis or matrix, but it can be removed by acids without destroying the general shape of the bone; and, after the removal of its inorganic salts, a bone is left soft, tough, and flexible.

The phosphates of potassium and sodium with the carbonates, maintain the alkalinity of the blood.

Carbonate of calcium occurs in bones and teeth, but in much smaller quantity than the phosphate (pp. 83 and 93). It is found also in some other parts. The small concretions of the internal ear (otoliths) are composed of crystalline carbonate of calcium, and form the only example of inorganic crystalline matter existing as such in the body.

The *carbonates of potassium* and *sodium* are found in the blood, and some other fluids and tissues.

The *sulphates of potassium, sodium*, and *calcium* are met with in small amount in most of the solids and fluids.

A very minute quantity of *silica* exists in the urine, and in the blood. Traces of it have been found also in bones, hair, and some other parts.

The especial place of *iron* is in hæmoglobin, the colouring-matter of the blood, of which a further account will be given with the chemistry of the blood. Peroxide of iron is found, in very small quantities, in the ashes of bones, muscles, and many tissues, and in lymph and chyle, albumin of serum, fibrin, bile, and other fluids; and a salt of iron, probably a phosphate, exists in the hair, black pigment, and other deeply coloured epithelial or horny substances.

Aluminium, Manganese, Copper, and *Lead.*—It seems most likely that in the human body, *copper, manganesium, aluminium,* and *lead* are merely accidental elements, which, being taken in minute quantities with the food, and not excreted at once with the fæces, are absorbed and deposited in some tissue or organ, of which, however, they form no necessary part. In the same manner, *arsenic*, being absorbed, may be deposited in the liver and other parts.

CHAPTER IV.

STRUCTURAL COMPOSITION OF THE HUMAN BODY.

By dissection, the human body can be proved to consist of various dissimilar parts, bones, muscles, brain, heart, lungs, intestines, &c., while, on more minute examination, these are found to be composed of various tissues, such as the connective, epithelial, nervous, muscular, and the like.

Embryology teaches us that all this complex organisation has been developed from a microscopic body about $\frac{1}{200}$ in. in diameter (ovum), which consists of a spherical mass of jelly-like matter enclosing a smaller spherical body (germinal vesicle). Further, each individual tissue can be shown largely to consist of bodies essentially similar to an ovum, though often differing from it very widely in external form. They are termed *cells:* and it must be at once evident that a correct knowledge of the nature and activities of the cell forms the very foundation of physiology.

Cells are, in fact, physiological no less than histological units.

The prime importance of the cell as an element of structure, was first established by the researches of Schleiden, and his conclusions drawn from the study of vegetable histology, were at once extended by Schwann to the animal kingdom. The earlier observers defined a cell as a more or less spherical body limited by a membrane, and containing a smaller body termed a *nucleus*, which in its turn encloses one or more *nucleoli*. Such a definition applies admirably to most vegetable cells, but the more extended investigation of animal tissues soon showed that in many cases no limiting membrane or cell-wall could be demonstrated.

Its presence or absence, therefore, was now regarded as quite a secondary matter, while at the same time the cell-substance came gradually to be recognised as of primary importance. Many of the lower forms of animal life, *e.g.*, the rhizopoda, were found to consist almost entirely of matter very similar in appearance and chemical composition to the cell-substance of higher forms: and this from its chemical resemblance to flesh was

termed Sarcode by Dujardin. When recognised in vegetable cells it was called Protoplasm by Mulder, while Remak applied the same name to the substance of animal cells. As the presumed formative matter in animal tissues it was termed Blastema, and in the belief that, wherever found, it alone of all substances has to do with generation and nutrition, Dr. Beale has named it "Germinal matter" or Bioplasm. Of these terms the one most in vogue at the present day is Protoplasm, and inasmuch as all life, both in the animal and vegetable kingdoms, is associated with protoplasm, we are justified in describing it with Huxley, as the "physical basis of life."

A cell may now be defined as a nucleated mass of protoplasm,* of microscopic size.

It is true that several lower forms of life recently described by Haeckel, Huxley, and others, consist of non-nucleated protoplasm, but the above definition holds good for all the higher plants and animals.

Hence a summary of the manifestations of cell-life is really an account of the vital activities of protoplasm. This must of course be preceded by a brief review of its physical and chemical characters.

Chemical characters.—Chemically, protoplasm is an extremely unstable albuminoid substance, insoluble in water, but becoming gelatinous by imbibition; by analysis it cannot be distinguished from ordinary albumen, though of course its power of growth, development, &c., constitute an essential distinction.

Physical characters.—Physically, protoplasm is viscid, varying in consistency from semi-fluid to strongly coherent.

All protoplasm, like albumen, undergoes heat stiffening or coagulation at about 130° Fah., and hence no organism can live when its own temperature is raised to this point, though, of course, many can exist for a time in an atmosphere much hotter than this, since they possess the means of regulating their own temperature. When it is examined under the microscope two varieties of protoplasm are recognised—the hyaline, and the granular. Both are alike transparent, but the former is perfectly

* In the human body the cells range from the red blood-cell ($\frac{1}{3000}$ in.) to the ganglion-cell ($\frac{1}{300}$ in.).

homogeneous, while the latter (the more common variety) contains small granules or molecules of various sizes and shapes: they usually appear dark when viewed with transmitted light, they seem lighter than water, and many are soluble in ether: these latter consist probably of fatty matter.

Physiological characters.—These may be conveniently treated under the three heads of motion, nutrition, and reproduction.

I. *Motion.*—It is probable that the protoplasm of all cells is capable at some time of exhibiting movement: at any rate this phenomenon, which not long ago was regarded as quite a curiosity, has been recently observed in cells of many different kinds.

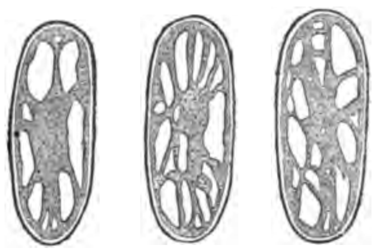
It may be readily studied in the Amœbæ, in the colourless blood-cells of all vertebrata, in the branched cornea-cells of the frog, in the hairs of the stinging-nettle and Tradescantia, and the cells of Vallisneria and Chara.

These motions may be divided into two classes—Fluent and Ciliary.

Another variety—the molecular or vibratory—has also been classed by some observers as vital, but it seems exceedingly probable that it is nothing more than the well-known "Brownian" molecular movement, a purely mechanical phenomenon which may be observed in any minute particles, *e.g.*, of gamboge, suspended in a fluid of suitable density, such as water. Such particles are seen to oscillate rapidly to and fro, and not to progress in any definite direction.

Fluent.—This movement of protoplasm is rendered perceptible (1) by the motion of the granules, which are nearly always imbedded in it, and (2) by changes in the outline of its mass.

Fig. 1.*



If part of a hair of Tradescantia (fig. 1) be viewed under a high magnifying power, streams of protoplasm containing

* Fig. 1. Cell of Tradescantia drawn at successive intervals of two minutes. The cell-contents consist of a central mass connected by many irregular processes to a peripheral film: the whole forms a vacuolated mass of protoplasm, which is continually changing its shape (Schofield).

crowds of granules hurrying along, like the foot-passengers in a busy street, are seen flowing steadily in definite directions, some coursing round the film which lines the interior of the cell-wall, and others flowing towards or away from the irregular mass in the centre of the cell-cavity.

Many of these streams of protoplasm run together into larger ones, or are lost in the central mass, and thus ceaseless variations of form are produced.

In the Amœba, a minute animal, consisting of a shapeless and structureless mass of sarcode, an irregular mass of protoplasm is gradually thrust out from the main body and retracted: a second mass is then protruded in another direction, and gradually the whole protoplasmic substance is, as it were, drawn into it. The Amœba thus comes to occupy a new position, and when this is repeated several times we have locomotion in a definite direction,

*Fig. 2.**

together with a continual change of form. These movements, when observed in other cells, such as the colourless blood corpuscles of higher animals (fig. 2) are hence termed *amœboid*.

Colourless blood corpuscles were first observed to migrate, *i.e.*, pass through the walls of the bloodvessels, by Waller, whose observations were confirmed and extended to connective tissue corpuscles by the researches of Recklinghausen, Cohnheim, and others, and thus the phenomenon of migration has been proved to play an important part in many normal, and pathological processes, especially in that of inflammation.

This amœboid movement enables many of the lower animals to capture their prey, which they accomplish by simply flowing round and enclosing it.

The remarkable motions of pigment-granules observed in the branched pigment-cells of the frog's skin by Lister, are probably due to amœboid movement. These granules are seen at one time

* Fig. 2. Human colourless blood-corpuscle, showing its successive changes of outline within ten minutes when kept moist on a warm stage (Schofield).

distributed uniformly through the body and branched processes of the cell, while under the action of various stimuli (*e.g.*, light and electricity) they collect in the central mass, leaving the branches quite colourless.

Ciliary action must be regarded as only a special variety of the general motion with which all protoplasm is endowed.

The grounds for this view are the following: In the case of the Infusoria, which move by the vibration of cilia (microscopic hair-like processes projecting from the surface of their bodies) it has been proved that these are simply processes of their protoplasm protruding through pores of the investing membrane, like the oars of a galley, or the head and legs of a tortoise from its shell: certain reagents cause them to be partially retracted.

Moreover, in some cases cilia have been observed to develop from, and in others to be transformed into, amœboid processes.

The movements of protoplasm can be very largely modified or even suspended by external conditions, of which the following are the most important.

1. *Changes of temperature.*—Moderate heat acts as a stimulant: this is readily observed in the activity of the movements of a human colourless blood-corpuscle when placed under conditions in which its normal temperature and moisture are preserved.

Extremes of heat and cold stop the motions entirely.

2. *Mechanical stimuli.*—When gently squeezed between a cover and object glass under proper conditions, a colourless blood-corpuscle is stimulated to active amœboid movement.

3. *Nerve-influence.*—By stimulation of the nerves of the Frog's cornea, contraction of certain of its branched cells has been produced.

4. *Chemical stimuli.*—Water generally stops amœboid movement and by imbibition causes great swelling and finally bursting of the cells.

In some cases, however, (myxomycetes) protoplasm can be almost entirely dried up and is yet capable of renewing its motions when again moistened.

Dilute salt-solution, and many dilute acids and alkalies, stimulate the movements temporarily.

Ciliary movement is suspended in an atmosphere of hydrogen or carbonic acid, and resumed on the admission of air or oxygen.

5. *Electrical.*—Weak currents stimulate the movement, while strong currents cause the corpuscles to assume a spherical form and become motionless.

II. *Nutrition.*—The nutrition of cells will be more appropriately described in the chapter on Nutrition and Secretion.

Before describing the reproduction of cells it will be necessary to consider more at length their structure.

Cell-wall.—We have seen (p. 43) that the presence of a limiting-membrane is no essential part of the definition of a cell.

In nearly all cells the outer layer of the protoplasm attains a firmer consistency than the deeper portions: the individuality of the cell becoming more and more clearly marked as this cortical layer becomes more and more differentiated from the deeper portions of cell-substance. Side by side with this physical, there is a gradual chemical differentiation, till at length, as in the case of the fat cells (p. 75), we have a definite limiting membrane differing chemically as well as physically from the cell-contents, and remaining as a shrivelled-up bladder when they have been removed. Such a membrane is transparent and structureless, flexible, and permeable to fluids.

The cell-substance can, therefore, still be nourished by imbibition through the cell-wall. In many cases (especially in fat) a membrane of some toughness is absolutely necessary to give to the tissue the requisite consistency. When these membranes attain a certain degree of thickness and independence they are termed capsules: as examples, we may cite the capsules of cartilage-cells (p. 80), and the thick, tough envelope of the ovum termed the "primitive chorion."

Cell-contents.—In accordance with their respective ages, positions, and functions, the contents of cells are very varied.

The original protoplasmic substance may undergo many transformations; thus, in fat cells we may have oil, or fatty crystals, occupying nearly the whole cell cavity: in pigment cells we find granules of pigment; in the various gland cells the elements of their secretions. Moreover, the original protoplasmic contents of the cell may undergo a gradual chemical change with advancing age; thus the protoplasmic cell-substance of the deeper layers of the epidermis (p. 59) becomes gradually converted into keratin as the cell approaches the surface. So, too, the original protoplasm of the embryonic blood-cells is replaced by the hæmoglobin of the mature-coloured blood corpuscle.

Vegetable cells afford excellent examples of similar transfor-

mations in accordance with the age of the cell and its functions in the economy of the plant: thus we have starch, sugar, gum, and various acids produced and stored up.

So, too, by the deposition of successive layers of lignin on the inner surface of the cell-wall the primitive cavity is obliterated and the cell replaced by a laminated woody material.

Nucleus.—Nuclei (fig. 7, *a*) were first pointed out in the year 1833, by Dr. Robert Brown, who observed them in vegetable cells. They are either small transparent vesicular bodies containing one or more smaller particles (nucleoli), or they are semi-solid masses of protoplasm. In their relation to the life of the cell they are certainly hardly second in importance to the protoplasm itself, and thus Dr. Beale is fully justified in comprising both under the term "germinal matter." They exhibit their vitality, not in amœboid movements, but by initiating the process of division of the cell into two or more cells (fission) by first themselves dividing. Amœboid movement has, however, in one case been observed in nucleoli (Kidd).

Histologists have long recognised nuclei by two important characters:—

(1.) Their power of resisting the action of various acids and alkalies, particularly acetic acid, by which their outline is more clearly defined, and they are rendered more easily visible.

(2.) Their quality of staining in solutions of carmine, hæmatoxylin, &c. Nuclei are most commonly oval or round, and do not generally conform to the diverse shapes of the cells; they are altogether less variable elements than cells, even in regard to size, of which fact one may see a good example in the uniformity of the nuclei in cells so multiform as those of epithelium.

Their position in the cell is very variable. In many cells, especially where active growth is progressing, two or more nuclei are present.

III. *Reproduction.*

The life of individual cells is probably very short in comparison with that of the organism they compose: and their constant decay and death necessitate constant reproduction. The mode in which this takes place has long been the subject of great controversy.

In the case of plants, all of whose tissues are either cellular, or composed of cells which are modified or have coalesced in various ways, the theory that all new cells are derived from pre-existing ones was early advanced and very generally accepted. But in the case of animal tissues Schwann and others maintained a theory of spontaneous or free cell-formation.

According to this view a minute corpuscle (the future nucleolus) springs up spontaneously in a structureless inter cellular substance (blastema) very much as a crystal is formed in a solution. This nucleolus attracts the surrounding molecules of matter to form the nucleus, and by a repetition of the process the substance and wall of the cell are produced.

This theory, once almost universally current, was first disputed and finally overthrown by Remak and Virchow, whose researches established the truth expressed in the words "Omnis cellula e cellulâ."

It will be seen that this view is in strict accordance with the truth established much earlier in Vegetable Histology that every cell is descended from some pre-existing (mother-) cell. This derivation of cells from cells takes place by (1) fission or (2) gemmation.

The latter method has not been observed in the human body or the higher animals, and therefore requires but a passing notice. It consists essentially in the budding off and separating of a portion of the parent cell.

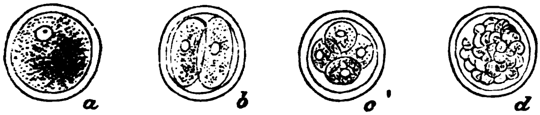
The former must now be briefly described. As typical examples we may select the ovum, the blood cell, and cartilage cells.

Ovum.—In the frog's ovum (in which the process can be most readily observed) after fertilization has taken place, there is first some amœboid movement, the oscillation gradually increasing until a permanent dimple appears, which gradually extends into a furrow running completely round the spherical ovum, and deepening until the entire yelk-mass is divided into two hemispheres of protoplasm each containing a nucleus (fig. 3, *b*). This process being repeated by the formation of a second furrow at right angles to the first, we have four cells produced (*c*): this

subdivision is carried on till the ovum has been divided by segmentation into a mass of cells (mulberry-mass) (*d*) out of which the embryo is developed.

Segmentation is the first step in the development of most animals, and doubtless takes place in man.

Fig. 3.*



Blood-cells.—Multiplication by fission has been observed in the colourless blood-cells of many animals. In some cases (fig. 4), the process has been seen to commence with the nucleolus which divides within the nucleus. The nucleus then elongates,

Fig. 4.†

and soon a well-marked constriction occurs, rendering it hour-glass shaped, till finally it is separated into two parts, which gradually recede from each other: the same process is repeated in the cell-substance, and at length we have two cells produced which by rapid growth soon attain the size of the parent-cell. In some cases there is a primary fission into three instead of the usual two cells.

Cartilage.—In cartilage (fig. 5), a process essentially similar occurs with the exception that (as in the ovum) the cells produced by fission remain in the original capsule, and in their turn undergo division, so that a large number of cells are sometimes observed within a common envelope. This process of fission within a capsule has been by some described as a separate

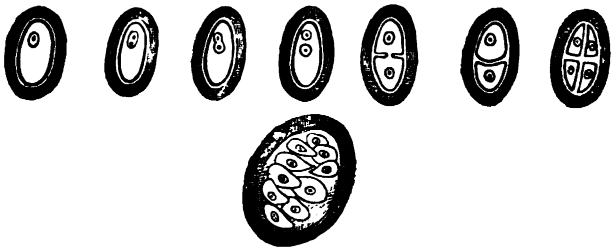
* Fig. 3. Diagram of an ovum (*a*) undergoing segmentation. In (*b*) it has divided into two; in (*c*) into four; and in (*d*) the process has ended in the production of the so-called "mulberry mass" (Frey).

† Fig. 4. Blood-corpuscle from a young deer embryo, multiplying by fission (Frey).

method, under the title "endogenous fission," but there seems to be no sufficient reason for drawing such a distinction.

It is important to observe that fission is often accomplished with great rapidity, the whole process occupying but a few

Fig. 5.*



minutes, hence the comparative rarity with which cells are seen in the act of dividing.

Functions of Cells.—The functions of cells are almost infinitely varied and make up nearly the whole of Physiology. They will be more appropriately considered in the chapters treating of the several organs and systems of organs which the cells compose.

Decay and Death of Cells.—There are two chief ways in which the comparatively brief existence of cells is brought to an end. (1) Mechanical abrasion, (2) Chemical transformation.

Mechanical abrasion.—The various epithelia furnish abundant examples. As it approaches the free surface the cell becomes more and more flattened and scaly in form and more horny in consistency, till at length it is simply rubbed off as in the epidermis.

Hence we find epithelial cells in the mucus of the mouth, intestine and genito-urinary tract. In the secretion of mucus the epithelial cells generally discharge their contents (mucin) and then the cell-membrane is broken up.

Chemical transformation.—In this case the cell-contents undergo

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* Fig. 5. Diagram of a cartilage cell undergoing fission within its capsule. The process of division is represented as commencing in the nucleolus, extending to the nucleus, and at length involving the body of the cell (Frey).

a degeneration which, though it may be pathological, is very often a normal process.

Thus we have (a) *fatty* metamorphosis producing oil-globules in the secretion of milk, fatty degeneration of the muscular fibres of the uterus after the birth of the fœtus, and of the cells of the Graafian follicle giving rise to the "corpus luteum." (See chapter on Generation.)

(b) *Pigmentary* degeneration from deposit of pigment, as in the epithelium of the air-vesicles of the lungs.

(c) *Calcareous* degeneration which is common in the cells of many cartilages.

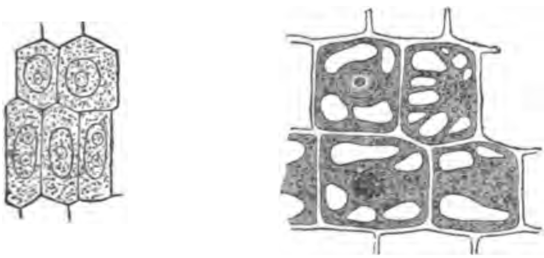
Having thus reviewed the life-history of cells in general, we may now discuss the leading varieties of form which they present.

In passing, it may be well to point out the main distinctions between animal and vegetable cells.

It has been already mentioned that in animal cells an envelope or cell-wall is by no means always present. In adult vegetable cells, on the other

*Fig. 6.**

A B



hand, a well-defined cellulose wall is highly characteristic: this, it should be observed, is non-nitrogenous, and thus differs chemically as well as structurally from the contained mass.

Moreover, in vegetable cells (fig. 6, B), the protoplasmic contents of the cell fall into two subdivisions: (1) a continuous film which lines the interior of the cellulose wall; and (2) a reticulate mass containing the nucleus and

* Fig. 6 (A). Young vegetable cells, showing cell-cavity entirely filled with granular protoplasm enclosing a large oval nucleus, with one or more nucleoli.

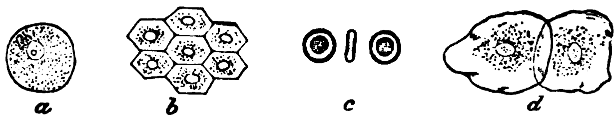
(B.) Older cells from same plant, showing distinct cellulose-wall and vacuolation of protoplasm.

occupying the cell-cavity; its interstices are filled with fluid. In young vegetable cells such a distinction does not exist; a finely granular protoplasm occupies the whole cell-cavity (fig. 6, A).

Another striking difference is the frequent presence of a large quantity of intercellular substance in animal tissues, while in vegetables it is comparatively rare, the requisite consistency being given to their tissues by the tough cellulose walls, often thickened by deposits of lignin. In animal cells this end is attained by the deposition of lime-salts in a matrix of intercellular substance, as in the process of ossification.

Forms of Cells.—Starting with the spherical or spheroidal (fig. 7, *a*) as the typical form assumed by a free cell, we find this altered to a polyhedral shape when the pressure on the cells in all directions is nearly the same (fig. 7, *b*).

*Fig. 7.**



Of this, the primitive segmentation-cells may afford an example.

The discoid shape is seen in blood-cells (fig. 7, *c*), and the scale-like form in superficial epithelial cells (fig. 7, *d*).

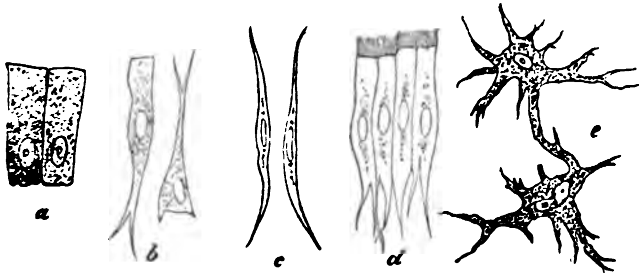
In some squamous cells (ridge and furrow cells) the cell-wall becomes, as it were, cogged, the processes of one cell fitting into corresponding depressions in an adjoining one, like bristles of two brushes which are pressed together (fig. 11).

Cylindrical, conical, or prismatic cells occur in the deeper layers of laminated epithelium, and the simple cylindrical epithelium of the intestine and many gland ducts. Such cells may taper off at one or both ends into fine processes, in the former case being caudate, in the latter fusiform (fig. 8). They may be greatly elongated so as to become fibres. Ciliated cells (figs. 19, 20) must be noticed as a distinct variety: they possess, but only on their free surfaces, hair-like processes (cilia). These vary immensely in size, and may even exceed in length the cell itself.

* Fig. 7. Various forms of cells. *a.* Spheroidal, showing nucleus and nucleolus. *b.* Polyhedral. *c.* Discoidal (blood cells). *d.* Scaly or squamous (epithelial cells).

Finally we have the branched or stellate cells, of which the large nerve-cells of the spinal cord, and the connective tissue corpuscle are typical examples (fig. 8, *e*). In these cells the primitive

Fig. 8.*



branches by secondary branching may give rise to an intricate network of processes.

Cells may be classified in many ways.

According to Form, they may be classified into spheroidal or polyhedral, discoidal, flat or scaly, cylindrical, caudate, fusiform, ciliated and stellate.

According to Situation, we may divide them into blood cells, gland cells, connective tissue cells, &c.

According to Contents, into fat and pigment cells and the like.

According to Function, into secreting, protective, contractile, &c.

According to their Origin into hypoblastic, mesoblastic, and epiblastic cells. (See chapter on Generation.)

It remains only to consider the various ways in which cells are connected together to form tissues, and the transformations by which intercellular substance, fibres and tubules are produced.

Modes of connection.—Cells are connected :—

(1) By a cementing intercellular substance. This is probably always present even between the closely apposed cells of cylin-

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* Fig. 8. Various forms of cells. *a.* Cylindrical or columnar. *b.* Caudate. *c.* Fusiform. *d.* Ciliated (from trachea). *e.* Branched, stellate.

drical epithelium, while in the case of cartilage it forms the main bulk of the tissue, and the cells only appear as imbedded in, not as cemented by, the intercellular substance.

This intercellular substance may be either homogeneous or fibrillated.

In many cases (*e.g.* the cornea) it can be shown to contain a number of irregular branched cavities, which communicate with each other, and in which the branched cells lie: through these branching spaces nutritive fluids can find their way into the very remotest parts of a non-vascular tissue.

As a special variety of intercellular substance must be mentioned the basement membrane (*membrana propria*) which is found at the base of the epithelial cells in most mucous membranes, and especially as an investing tunic of gland follicles which determines their shape, and which may persist as a hyaline saccule after the gland-cells have all been discharged.

(2) By anastomosis of their processes.

This is the usual way in which stellate cells, *e.g.* of the cornea, are united: the individuality of each cell is thus to a great extent lost by its connection with its neighbours to form a reticulum: as an example of a network so produced, we may cite the stroma of lymphatic glands.

Sometimes the branched processes breaking up into a maze of minute fibrils, adjoining cells are connected by an intermediate reticulum: this is the case in the nerve-cells of the spinal cord.

Besides the Cell, which may be termed the primary tissue-element, there are materials which may be termed secondary or derived tissue-elements. Such are Intercellular substance, Fibres and Tubules.

Intercellular substance is probably in all cases directly derived from the cells themselves. In some cases (*e.g.* cartilage), by the use of re-agents the cementing intercellular substance is, as it were, analysed into various masses, each arranged in concentric layers around a cell or group of cells, from which it was probably derived (fig. 35).

Fibres.—In the case of the crystalline lens, and of muscle

both striated and non-striated, each fibre is simply a metamorphosed cell: in the case of striped fibre the elongation being accompanied by a multiplication of the nuclei.

The various fibres and fibrillæ of connective tissue result from a gradual transformation of an originally homogeneous intercellular substance. Fibres thus formed may undergo great chemical as well as physical transformation: this is notably the case with yellow elastic tissue, in which the sharply defined elastic fibres, possessing great power of resistance to re-agents, contrast strikingly with the homogeneous matter from which they are derived.

Tubules which were originally supposed to consist of structureless membrane, have now, by the action of nitrate of silver, been proved in many cases to be composed of flat, thin cells, cohering along their edges. (See Capillaries.) The boundaries between the cells are marked out by the precipitation of oxide of silver under the action of light. In this way the composite structure of blood- and lymph-capillaries has been clearly demonstrated.

With these simple materials the various parts of the body are built up; the more elementary tissues being, so to speak, first compounded of them; while these again are variously mixed and interwoven to form more intricate combinations.

Thus are constructed epithelium and its modifications, connective tissue, fat, cartilage, bone, the fibres of muscle and nerve, &c.; and these, again, with the more simple structures before mentioned, are used as materials wherewith to form arteries, veins, and lymphatics, secreting and vascular glands, lungs, heart, liver and other parts of the body.

CHAPTER V.

STRUCTURE OF THE ELEMENTARY TISSUES.

In this chapter the leading characters and chief modifications of two great groups of tissues—the Epithelial and Connective—will be briefly described; while the Nervous and Muscular, together with several other more highly specialized tissues, will be appropriately considered in the chapters treating of their physiology.

Epithelium.

Epithelium is composed of cells of various shapes held together by a small quantity of cementing intercellular substance.

Epithelium clothes the whole exterior surface of the body, forming the epidermis with its appendages—nails and hairs; becoming continuous at the chief orifices of the body—nose, mouth, anus, and urethra—with the epithelium which lines the whole length of the alimentary and genito-urinary tracts, together with the ducts of their various glands. Epithelium also lines the cavities of the brain and the central canal of the spinal cord, the serous and synovial membranes, and the interior of all blood-vessels and lymphatics.

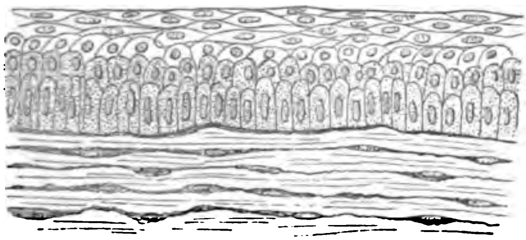
The cells composing it may be arranged in either one or more layers, so that it may be sub-divided into (*a*) Simple, and (*b*) Laminated epithelium. A simple epithelium, for example, lines the whole intestinal mucous membrane from the stomach to the anus: the epidermis on the other hand is laminated throughout its entire extent.

Epithelial cells may be conveniently classified as: 1.—Squamous, scaly, pavement, or tessellated. 2.—Spheroidal, glandular, or polyhedral. 3.—Columnar, cylindrical, conical, or goblet-shaped. 4.—Ciliated.

Although, for convenience, epithelial cells are thus classified, yet the first three forms of cells are sometimes met with at different depths in the same membrane. As an example of such

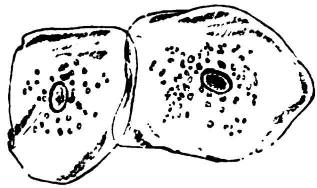
a laminated epithelium showing these different cell-forms at various depths, we may select the anterior epithelium of the cornea (fig. 9).

Fig. 9.*

a
b


1. *Squamous Epithelium* (fig. 10).—Arranged in several superposed layers, this form of epithelium covers the skin, where it is called the Epidermis, and lines the mouth, pharynx, and œsophagus, the conjunctiva covering the eye, the vagina, and entrance of the urethra in both sexes; while, as a single layer, the same kind of epithelium forms the innermost stratum of the choroid, and lines the interior of the serous and synovial sacs, and of the heart, blood- and lymph-vessels. It consists of cells, which are flattened and scaly, with an irregular outline: and, when laminated, may form a dense horny investment, as on parts of the palms of the hands and soles of the feet. The nucleus is often not apparent, though it can generally be rendered visible by the use of caustic potash. The really cellular nature of even the dry and shrivelled scales cast off from the surface of the epidermis, can be proved by the application of this re-agent, which causes them rapidly to swell and assume their originally spheroidal form.

Fig. 10.†

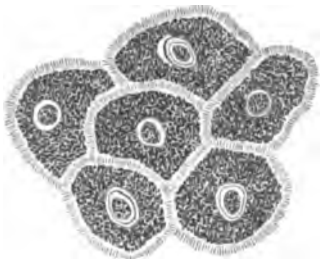


* Fig. 9. Vertical section of Rabbit's cornea. *a.* Anterior epithelium, showing the different shapes of the cells at various depths from the free surface. *b.* Portion of the substance of cornea (Klein).

† Fig. 10. Epithelium scales from the inside of the mouth. × 260. (Henle.)

Squamous cells are generally united by an intercellular substance; but in many of the deeper layers of epithelium in the mouth and skin, the outline of the cells is very irregular, (fig. 11) and the cells are as it were interlocked—the processes of one cell fitting into depressions in the adjoining ones.

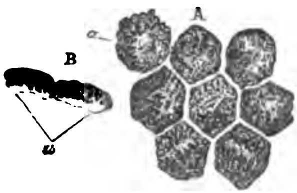
Fig. 11.*



The way in which these "ridge and furrow," or "cogged" cells are held together, has been differently explained by Mr. Martin, who maintains that the interlocking is only apparent, and that the processes meet end to end and are fused together, and that consequently the cells can only be separated by breaking across these processes.

Squamous epithelium, *e.g.*, the cells of the choroid, may have a deposit of pigment in the cell-substance. This pigment consists of minute molecules of *melanin*, imbedded in the cell-substance and almost concealing the nucleus, which is itself transparent (fig. 12).

Fig. 12.†



In albino rabbits, in which the pigment of the choroid is absent, this layer is found to consist of colourless pavement epithelial cells.

The squamous epithelium lining the serous membranes, and the interior of blood-vessels, presents so many special features as to demand a special description; by some histologists it is even called by a distinct name—Endothelium.

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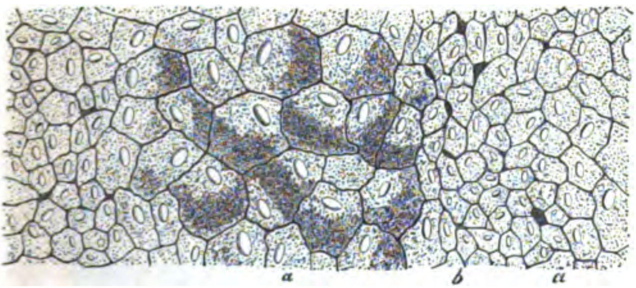
* Fig. 11. Jagged cells of the middle layers of pavement epithelium, from a vertical section of the gum of a newborn infant (Klein).

† Fig. 12. Pigment-cells from the choroid. A, cells still cohering, seen on their surface; *a*, nucleus indistinctly seen. In the other cells the nucleus is concealed by the pigment granules. B, two cells seen in profile; *a*, the outer or posterior part containing scarcely any pigment. × 370. (Henle.)

The main points of distinction above alluded to are, 1. the very flattened form of these cells; 2. their constant occurrence in only a single layer; 3. the fact that they are developed from the "mesoblast," while all other epithelial cells are derived from the "epiblast," or "hypoblast." (See chapter on Generation.) Endothelial cells form an important and well-defined subdivision of squamous epithelial cells, which has been especially studied during the last few years. Their examination has been much facilitated by the adoption of the method of staining serous membranes with nitrate of silver.

When a small portion of a perfectly fresh serous membrane, as the mesentery or omentum, is immersed for a few minutes in a quarter per cent. solution of this re-agent, washed with water and exposed to the action of light, the silver oxide is precipitated along the boundaries of the cells, and the whole surface is found to be marked out with exquisite delicacy, by fine dark lines, into a number of polygonal spaces (endothelial cells) (fig. 13).

Fig. 13.*



Endothelium lines all the serous cavities of the body, including the anterior chamber of the eye, also the synovial membranes of joints, and the interior of the heart and of all blood-vessels and lymphatics. It forms also a delicate investing sheath for nerve-fibres and peripheral ganglion-cells.

* Fig. 13. Abdominal surface of centrum tendineum of rabbit, showing the general polygonal shape of the endothelial cells: each is nucleated (Klein). × 300.

Endothelial cells are scaly in form, and irregular in outline; those lining the interior of blood-vessels and lymphatics having a spindle-shape with a very wavy outline. They enclose a clear, oval nucleus, which, when the cell is viewed in profile, is seen to project from its surface.

Endothelial cells may be ciliated, *e.g.*, those in the mesentery of frogs, especially about the breeding season.

Besides the ordinary endothelial cells above described, there are found on the omentum and parts of the pleura of many animals, little bud-like processes or nodules, consisting of small

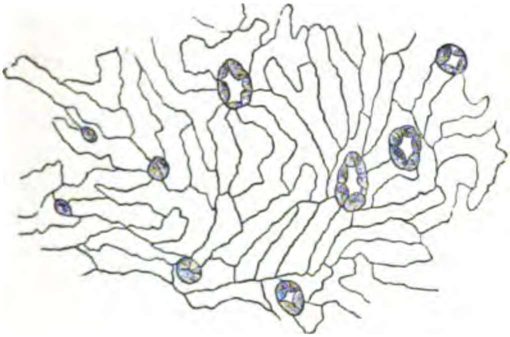
Fig. 14.*

polyhedral granular cells, rounded on their free surface, which multiply very rapidly by division (fig. 14). These constitute what is known as "germinating endothelium." The process of germination doubtless goes on in health, and the small

* Fig. 14. Silver-stained preparation of great omentum of dog, which shows, amongst the flat endothelium of the surface, small and large groups of germinating endothelium, between which numbers of stomata are to be seen (Klein). × 300.

cells which are thrown off in succession are carried into the lymphatics. The buds may be enormously increased both in

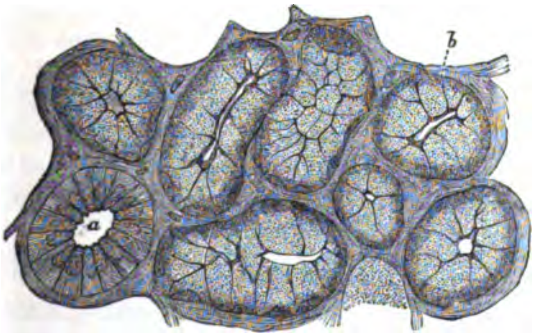
Fig. 15.*



number and size, in certain diseased conditions. (Klein, Burdon-Sanderson.)

On those portions of the peritoneum and other serous mem-

Fig. 16.†



branes where lymphatics abound, there are numerous small orifices—*stomata*—(fig. 15) between the endothelial cells: these

* Fig. 15. Peritoneal surface of septum cisternæ lymphaticæ magnæ of frog. The stomata, some of which are open, some collapsed, are surrounded by germinating endothelium (Klein). × 160.

† Fig. 16. Section of submaxillary gland of dog. *a*. Salivary duct, with columnar epithelium. *b*. Spheroidal or glandular epithelium lining follicle. (Kölliker.)

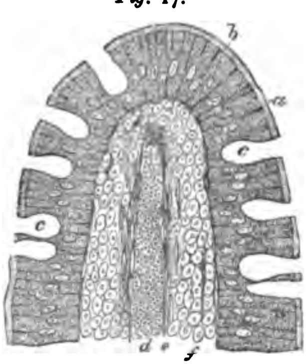
are really the open mouths of lymphatic vessels, and through them lymph-corpuscles, and the serous fluid from the serous cavity, pass into the lymphatic system.

2. *Spheroidal* epithelial cells are the active secreting agents in most secreting glands, and thence are often termed glandular: they are generally more or less rounded in outline: often polygonal from mutual pressure.

Excellent examples are to be found in the secreting tubes of the kidney, and in the salivary and peptic glands (fig. 16).

3. *Columnar* epithelium (fig. 17, *b*) lines the mucous membrane of the stomach and intestines, from the cardiac orifice of the stomach to the anus, and wholly or in part the ducts of the glands opening on its free surface; also many gland-ducts in other regions of the body, *e.g.*, mammary, salivary, &c.; further, it lines the uterine mucous membrane, and forms the deeper layers of the epithelial lining of the trachea and oviducts.

Fig. 17.*



It consists of cells which are approximately cylindrical or prismatic in form, and contain a large oval nucleus. When evenly packed side by side as a single layer, the cells are uniformly columnar; but when occurring in several layers as in the deeper strata of the epithelial lining of the trachea, their shape is very variable, and often departs very widely from the typical columnar form.

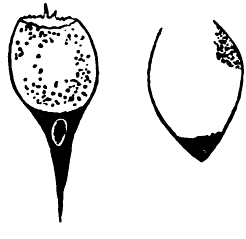
Goblet cells.—Many cylindrical epithelial cells undergo a curious transformation, and from the alteration in their shape are termed goblet-cells (fig. 17, *c*, and 18).

These are never seen in a perfectly fresh specimen: but if such

* Fig. 17. Vertical section of a villus of the small intestine of a cat. *a*. Striated basal border of the epithelium. *b*. Columnar epithelium. *c*. Goblet cells. *d*. Central lymph-vessel. *e*. Smooth muscular fibres. *f*. Adenoid stroma of the villus in which lymph corpuscles lie (Klein).

a specimen be watched for some time, little knobs are seen gradually appearing on the free surface of the epithelium, and are finally detached; these consist of the cell-contents which are discharged by the open mouth of the goblet, leaving the nucleus surrounded by the remains of the protoplasm in its narrow stem.

Fig. 18.*



Some regard this transformation as a normal process which is continually going on during life, the discharged cell-contents contributing to form the mucus of the alimentary canal, the cells being supposed in many cases to recover their original shape.

Some epithelia possess a structureless layer on their free surface, which may form a definite cuticular membrane: such a layer is present in the intestine, and appearing striated when viewed in section, is termed the "striated basilar border" (fig. 17).

4. *Ciliated* cells are generally cylindrical (fig. 20), but may be spheroidal or even almost squamous in shape (fig. 19).

Fig. 19.†

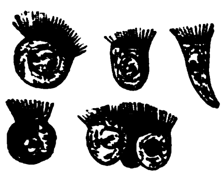


Fig. 20.‡

This form of epithelium lines the whole of the respiratory tract from the larynx to the finest sub-divisions of the bronchi, also the lower parts of the nasal passages, and some portions of the generative apparatus—in the male, lining the "vasa efferentia" of the testicle, and their prolongations as far as the lower end of

* Fig. 18. Goblet-cells (Klein).

† Fig. 19. Spheroidal ciliated cells from the mouth of the frog; magnified 300 diameters (Sharpey).

‡ Fig. 20. Columnar ciliated epithelium cells from the human nasal membrane; magnified 300 diameters (Sharpey).

the epididymis; in the female commencing about the middle of the neck of the uterus, and extending throughout the uterus and Fallopian tubes to their fimbriated extremities, and even for a short distance on the peritoneal surface of the latter.

The ventricles of the brain and the central canal of the spinal cord are clothed with ciliated epithelium in the child, but in the adult it is limited to the central canal of the cord.

The *Cilia*, or fine hair-like processes which give the name to this variety of epithelium, vary a good deal in size in different classes of animals, being very much smaller in the higher than among the lower orders, in which they sometimes exceed in length the cell itself.

The number of cilia on any one cell ranges from ten to thirty, and those attached to the same cell are often of different lengths. When examined in a portion of living ciliated epithelium immersed in some indifferent fluid, they are seen to be in constant rapid motion; each cilium being fixed at one end, and swinging or lashing to and fro. The general impression given to the eye of the observer is very similar to that produced by waves in a field of corn, or swiftly running and rippling water, and the result of their movement is to produce a continuous current in a definite direction, and this direction is invariably the same on the same surface, being always, in the case of a cavity, towards its external orifice.

In addition to the above kinds of epithelium, certain highly specialized forms of epithelial cells are found in the organs of smell, sight, and hearing, viz., olfactory cells, retinal rods and cones, auditory cells; they will be described in the chapters which deal with their functions. (See Index.)

Functions of epithelium.—According to function, epithelial cells may be classified as:—

(1.) *Protective, e.g.*, in the skin, mouth, blood-vessels, &c.
(2.) *Protective and moving*—ciliated epithelium.

(3.) *Secreting*—glandular epithelium; or, *Secreting formed elements*—epithelium of testicle secreting spermatozoa.

(4.) *Protective and secreting, e.g.*, epithelium of intestine.

(5.) *Sensorial, e.g.*, olfactory cells, rods and cones, organ of Corti.

Epithelium forms a continuous smooth investment over the whole body, being thickened into a hard, horny tissue at the points most exposed to pressure, and developing various appendages, such as hairs and nails, whose structure and functions will be considered in a future chapter. Epithelium lines also the sensorial surfaces of the eye, ear, nose, and mouth, and thus serves as the medium through which all impressions from the external world—touch, smell, taste, sight, hearing—reach the delicate nerve-endings, whence they are conveyed to the brain.

The ciliated epithelium which lines the air-passages serves not only as a protective investment, but also by the movements of its cilia is enabled to propel fluids and minute particles of solid matter so as to aid their expulsion from the body. In the case of the Fallopian tube, this agency doubtless assists the progress of the ovum towards the cavity of the uterus. Of the purposes served by cilia in the ventricles of the brain, nothing is known. (For an account of the nature and conditions of ciliary motion, see chapter on Motion.)

The epithelium of the various glands, and of the whole intestinal tract, has the power of *secretion, i.e.*, of chemically transforming certain materials of the blood; in the case of mucus and saliva this has been proved to involve the transformation of the epithelial cells themselves; the cell substance of the epithelial cells of the intestine being discharged by the rupture of their envelopes, as mucus.

Epithelium is likewise concerned in the processes of transudation, diffusion, and absorption.

It is constantly being shed at the free surface, and reproduced in the deeper layers. The various stages of its growth and development can be well seen in a section of any laminated epithelium, such as the epidermis.

Connective Tissues.

This group of tissues forms the skeleton with its various connections—bones, cartilages, ligaments, &c.—and also affords a supporting framework and investment to various organs composed of nervous, muscular, and glandular tissue. Its chief function is the mechanical one of support, and for this purpose it is so intimately interwoven with nearly all the textures of the body, that if all other tissues could be removed, and the connective tissues left, we should have a wonderfully exact model of almost every organ and tissue in the body, correct even to the smallest minutiæ of structure.

The chief varieties of connective tissue may be conveniently represented in the following tabular view :—

Connective Tissues
- *Gelatinous*
- *Reticular*
- *Fibrous*
  - *White fibrous.*
  - *Yellow elastic.*
  - *Areolar.*
- *Adipose*
- *Cartilage*
- *Bone*

Connective tissue consists essentially of *cells* and *intercellular substance.* The cells are of various shapes, and the intercellular substance may be *homogeneous,* as in hyaline cartilage, *fibrillar,* as in white fibrous tissue, or *calcified,* as in bone. These tissue elements combined in different arrangements, give us the above varieties, which will be now considered in order.

1. *Gelatinous,* or mucoid.

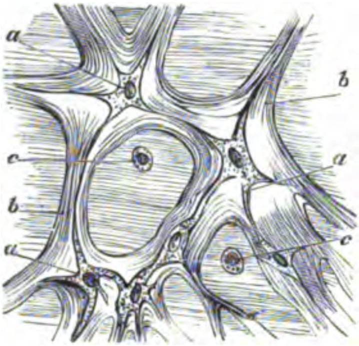
This, which is the simplest form of connective tissue, constitutes the chief part of the bodies of jelly-fish; it is found in many parts of the human embryo, but remains in the adult only in the vitreous humour of the eye.

It may be best seen in the vitreous humour, the "Whartonian jelly" of the umbilical cord, and the "enamel organ" of developing teeth.

It consists of cells, which in the vitreous humour are rounded,

in the jelly of the umbilical cord and in the enamel organ are stellate, imbedded in a soft semi-diffluent jelly-like intercellular substance which forms the bulk of the tissue, and which contains a considerable quantity of mucin (fig. 21).

Fig. 21.*

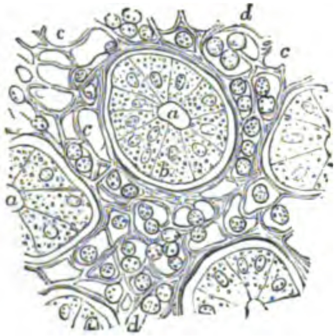


In the umbilical cord, that part of the jelly immediately surrounding the stellate cells shows marks of obscure fibrillation.

2. *Retiform.*

This is a special variety of connective tissue, consisting of a very delicate network of minute fibrils, formed by the union of processes of branched connective-tissue corpuscles (fig. 22). It composes the stroma of the spleen and lymphatic glands. A very delicate variety of connective tissue, allied to the retiform, and sometimes termed *neuroglia*, forms the supporting tissue in the brain, spinal cord, and retina.

Fig. 22.†



3. *Fibrous tissue* forms the periosteum and perichondrium, the aponeuroses, fasciæ, ligaments and tendons, the stroma of serous and mucous membranes, of the true skin, of the subserous and submucous tissues; it also occurs in the blood- and lymph-vessels and their sheaths, and in the endocardium, in the tunics of the

* Fig. 21. Tissue of the jelly of Wharton from umbilical cord. *a*, connective-tissue corpuscles; *b*, fasciculi of connective tissue; *c*, spherical formative cells (Frey).

† Fig. 22. Transverse section of mucous membrane of intestine. *a*, Lieberkühn's gland; *c*, and *d*, retiform tissue (Frey).

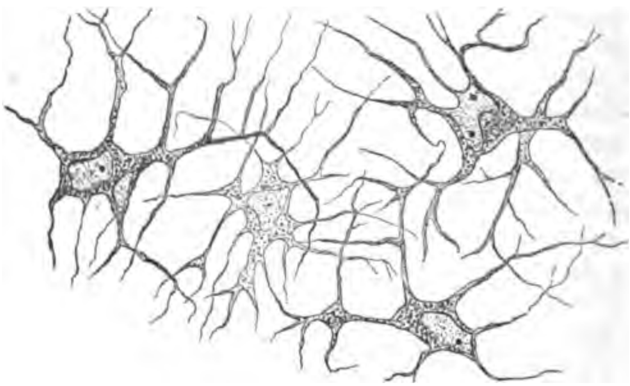
eye-ball, and as the interstitial connective tissue of most other organs.

The elements of fibrous tissue are Cells and Fibres.

Cells.—The cells are of two kinds—

(*a.*) *Branched cells.*—These are fixed cells of a flattened shape, with branched processes, which are often united together to form a network: they can be most readily observed in the cornea in which they are arranged, layer above layer, parallel to the free surface. They lie in spaces, which they accurately fill, and which form by anastomosis a system of branching canals freely communicating (fig. 23). These branched cells, in certain situa-

Fig. 23.*



tions, contain a number of pigment-granules, giving them a dark appearance: they form one variety of pigment-cells. Branched pigment-cells of this kind are found in the outer layers of the choroid (fig. 24).

In many lower animals, such as the frog, they are found widely distributed, not only in the skin, but also in many internal parts, *e.g.*, the mesentery and sheaths of blood-vessels.

In the web of the frog's foot such pigment cells may be seen, with pigment evenly distributed through the body of the cell and

* Fig. 23. Horizontal preparation of cornea of frog; showing the network of branched cornea corpuscles. The ground-substance is completely colourless. × 400. (Klein.)

its processes; but under the action of light, electricity, and other stimuli, the pigment-granules become massed in the body of the cell, leaving the processes quite hyaline; if the stimulus be removed, they will gradually be distributed again all over the processes. Thus the skin in the frog is sometimes uniformly dusky, and sometimes quite light-coloured, with isolated dark spots. In the choroid the pigment-cells absorb stray light.

Fig. 24.*

(*b.*) *Amœboid cells*, of an approximately spherical shape: they have a great general resemblance to colourless blood corpuscles (fig. 2), with which some of them are probably identical. They consist of finely granular nucleated protoplasm, and have the property, not only of changing their form, but also of moving about, whence they are termed migratory. They are readily distinguished from the branched connective-tissue corpuscles by their free condition, and the absence of processes.

Fibres.—These also are of two kinds—(*a.*) White fibres. (*b.*) Yellow elastic fibres.

(*a.*) *White Fibres.*—These are arranged parallel to each other in wavy bundles of various sizes: such bundles may either have a parallel arrangement (fig. 26, A), or may produce quite a felted texture by their interlacement. The individual fibres composing these fasciculi are homogeneous, unbranched, and of the same diameter throughout. They can readily be isolated by macerating a portion of white fibrous tissue (*e.g.*, a small piece of tendon) for a short time in lime, or baryta-water, or in a solution of common salt, or permanganate of potash: these reagents possessing the power of dissolving the cementing inter-fibrillar substance (which is nearly allied to syntonin), and thus separating the fibres from each other.

(*b.*) *Yellow elastic fibres* (fig. 26, B) are of all sizes, from exces-

* Fig. 24. Ramified pigment-cells, from the tissue of the choroid coat of the eye; magnified 350 diameters. *a*, cells with pigment; *b*, colourless fusiform cells (Kölliker).

sively fine fibrils up to fibres of considerable thickness: they are distinguished from white fibres by the following characters:—(1.) Their great power of resistance even to the prolonged action of chemical reagents, *e.g.*, Caustic Soda, Acetic Acid, &c. (2.) Their well-defined outlines. (3.) Their great tendency to branch and form networks by anastomosis. (4.) They very often have a twisted corkscrew-like appearance, and their

Fig. 25.*

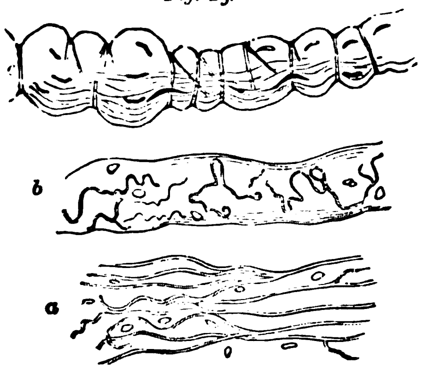
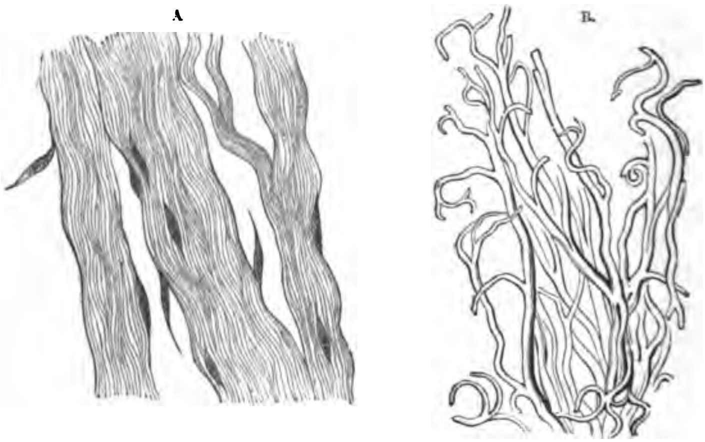


Fig. 26.†



* Fig. 25. Magnified view of areolar tissue (from different parts) treated with acetic acid. The white filaments are no longer seen, and the yellow or elastic fibres with the nuclei come into view. At *c*, elastic fibres wind round a bundle of white fibres, which, by the effect of the acid, is swollen out between the turns. Some connective-tissue corpuscles are indistinctly represented in *c* (Sharpey).

† Fig. 26. A. Mature white fibrous tissue of tendon, consisting mainly of fibres with a few scattered fusiform cells (Stricker). B. Elastic fibres from the ligamenta subflava, magnified about 200 diameters (Sharpey).

free ends usually curl up. (5.) They are of a yellowish tint, and very elastic.

Areolar tissue consists of cells, and white and yellow fibres in various proportions; its elasticity depending, of course, upon the elastic fibres which it contains. When treated with acetic acid, the fasciculi of white fibres in areolar tissue swell up and lose their fibrillar appearance, becoming clear and transparent; while the nuclei and yellow elastic fibres come more plainly into view (fig. 25).

White fibrous tissue (fig. 26, A) occurs typically developed in tendons.

A tendon consists essentially of bundles of white fibres, with chains of cells among them. In a very young tendon these cells are of a quadrangular shape, and are arranged end to end, forming a chain of cells in the long axis of the tendon (fig. 27): these chains of cells partially ensheath the bundles of fibres.

Fig. 27*.

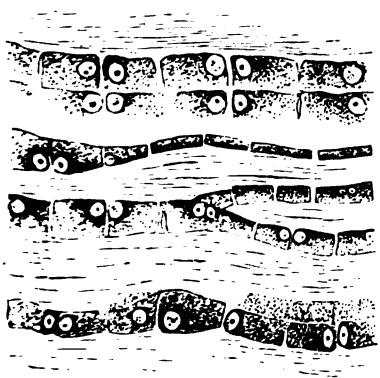
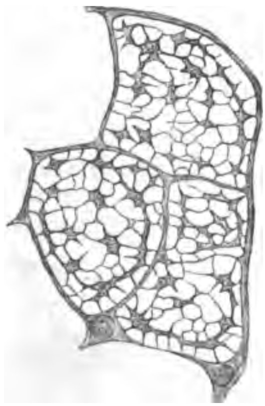


Fig. 28.†



In a mature tendon the cells become branched, and though no longer in such close apposition as before, they remain connected by a network of branched processes: this appearance is well shown in a transverse section of mature tendon (fig. 28).

* Fig. 27. Caudal tendon of young rat, showing the arrangement, form, and structure of the tendon cells. × 300. (Klein.)

† Fig. 28. Transverse section of tendon from a cross section of the tail of a rabbit. × 250. (Klein.)

Yellow Elastic Tissue.

We have seen that while tendons, fasciæ, and other inelastic structures consist almost exclusively of white fibrous tissue, elastic fibres are present in greater or less proportion in all forms of areolar connective tissue which have any appreciable degree of elasticity. If now the proportion of elastic fibres be increased so as to form the bulk of the tissue, we have an important variety of connective tissue termed "yellow elastic tissue." This occurs in the *ligamentum nuchæ* of lower animals (not in man), in the true vocal cords, in the ligamenta subflava, in arteries and veins, especially the larger arteries, in the lungs, trachea, and many other parts of the body.

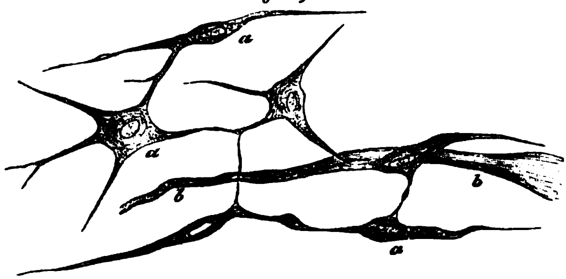
Elastic tissue as it occurs in the inner coats of arteries is, as a rule, no longer divisible into individual fibres, but consists of broad anastomosing elastic bands united so as to form a fenestrated membrane.

Development of Fibrous Tissue.

In the embryo the place of the fibrous tissues is at first occupied by a mass of roundish cells derived from the "mesoblast." (See chapter on Generation.)

These develop either into a network of branched cells, or into groups of fusiform cells (fig. 29).

Fig. 29.*



These branched and fusiform cells alike undergo a process of splitting, giving rise to fibres arranged in the one case in

* Fig. 29. Portion of submucous tissue of gravid uterus of sow. *a*, branched cells, more or less spindle-shaped; *b*, bundles of connective tissue (Klein).

interlacing networks (areolar tissue), in the other in parallel bundles (white fibrous tissue): the nuclei, surrounded by more or less of the protoplasm of the original cell, remain imbedded among the fibres. In the mature forms of purely fibrous tissue not only the remnants of the cell-substance, but even the nuclei may disappear. The embryonic tissue, from which *elastic* fibres are developed, is composed of fusiform cells, and a structureless intercellular substance by the gradual fibrillation of which elastic fibres are formed. The fusiform cells dwindle in size and eventually disappear so completely that in mature elastic tissue not a trace of them is to be found: meanwhile the elastic fibres steadily increase in size.

4. *Adipose Tissue.*

In almost all regions of the human body a larger or smaller quantity of adipose or fatty tissue is present; the chief exceptions being the subcutaneous tissue of the eyelids, penis, and scrotum, the nymphæ and the cavity of the cranium. Adipose *tissue* is also absent from the substance of many organs, as the lungs, liver, and others.

Fatty matter, not in the form of a distinct tissue, is also widely present in the body, as the fat of the liver and brain, of the blood and chyle, &c.

Adipose tissue is almost always found seated in areolar tissue, and forms in its meshes little masses of unequal size and irregular shape, to which the term, *lobules*, is commonly applied.

Fig. 30.*

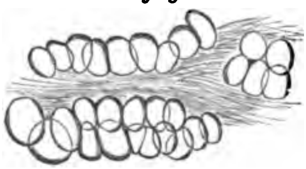
Under the microscope it is found to consist essentially of little vesicles or cells which present dark, sharply defined edges when viewed with transmitted light: they are about $\frac{1}{400}$ or $\frac{1}{300}$ of an inch in diameter, each composed of a structureless and colourless membrane or bag, filled with fatty matter, which is liquid during life, but in part solidified after death (fig. 30). A nucleus is always present in some part or

* Fig. 30. Ordinary fat-cells of a fat tract in the omentum of a rat (Klein).

other of the cell-wall, but in the ordinary condition of the cell it is not easily or always visible.

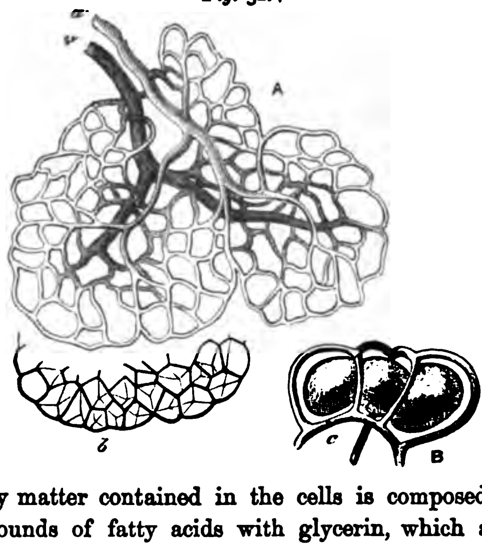
This membrane and the nucleus can generally be brought into view by staining the tissue: it can be still more satisfactorily demonstrated by extracting the contents of the fat-cells by ether, when the shrunken, shrivelled membranes remain behind. By mutual pressure, fat-cells come to assume a polyhedral figure (fig. 31).

Fig. 31.*



The ultimate cells are held together by capillary blood-vessels (fig. 32); while the little clusters thus formed are grouped into small masses, and held so, in most cases, by areolar tissue.

Fig. 32.†



The oily matter contained in the cells is composed chiefly of the compounds of fatty acids with glycerin, which are named

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* Fig. 31. Adipose tissue.

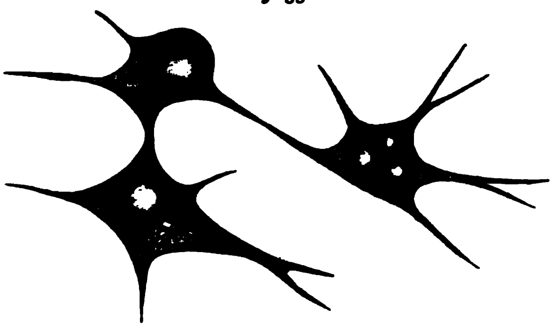
† Fig. 32. Blood-vessels of fat. A. Minute flattened fat-lobule, in which the vessels only are represented. *a*, the terminal artery; *v*, the primitive vein; *b*, the fat-vesicles of one border of the lobule separately represented. × 100. B. Plan of the arrangement of the capillaries (*c*) on the exterior of the vesicles: more highly magnified (Todd and Bowman).

olein, stearin, and palmitin. It is doubtful whether lymphatics or nerves are supplied to fat, although both pass through it on their way to other structures.

Development of Fat.

Fat-cells are developed from connective-tissue corpuscles: in the infra-orbital connective-tissue cells may be found exhibiting every intermediate gradation between an ordinary branched connective-tissue corpuscle and a mature fat-cell. The process of development is as follows: a few small drops of oil make their appearance in the protoplasm: by their confluence a larger drop is produced (fig. 33): this gradually increases in size at the expense of the original protoplasm of the cell, which becomes correspondingly diminished in quantity till in the mature cell it only forms a thin crescentic film, closely pressed against the cell-wall, and with a nucleus imbedded in its substance (fig. 30).

Fig. 33.*



Under certain circumstânces this process may be reversed and fat-cells may be changed back into connective-tissue corpuscles (Kölliker, Virchow).

Among the uses of fat, these seem to be the chief:—

1. It serves as a store of combustible matter which may be re-absorbed into the blood when occasion requires, and being burnt, may help to preserve the heat of the body.

2. That part of the fat which is situate beneath the skin must,

* Fig. 33. Branched connective-tissue corpuscles, developing into fat-cells (Klein).

by its want of conducting power, assist in preventing undue waste of the heat of the body by escape from the surface.

3. As a packing material, fat serves very admirably to fill up spaces, to form a soft and yielding yet elastic material wherewith to wrap tender and delicate structures, or form a bed with like qualities on which such structures may lie, unendangered by pressure.

As good examples of situations in which fat serves such purposes may be mentioned the palms of the hands, and soles of the feet, and the orbits.

4. In the long bones, fatty tissue, in the form known as marrow, serves to fill up the medullary canal, and to support the small blood-vessels which are distributed from it to the inner part of the substance of the bone.

5. *Cartilage.*—Cartilage or gristle exists in different forms in the human body, and has been classified under two chief heads, namely, *temporary* and *permanent* cartilage; the former term being applied to that kind of cartilage which, in the fœtus and in young subjects, is destined to be converted into bone. It may also be classified according to its histological characters under three heads, *cellular*, *hyaline*, and *fibrous*, the last being again capable of subdivision into two kinds—elastic or yellow cartilage, and the so-called fibro-cartilage. Elastic cartilage, however, contains fibres, and fibro-cartilage is more or less elastic; it will be well, therefore, for distinction's sake, to term those two kinds white fibro-cartilage and yellow fibro-cartilage respectively.

The accompanying table represents the classification of the varieties of cartilage:—

Cartilage ...	1. Temporary ...	(Either Cellular or Hyaline.)	
	2. Permanent ...	A. Cellular (not present in man).	
		B. Hyaline.	
		C. Fibrous .	White fibro-cartilage.
			Yellow fibro-cartilage.

All kinds of cartilage are composed of cells imbedded in a substance called the *matrix:* and the apparent differences of structure met with in the various kinds of cartilage are more

due to differences in the character of the matrix than of the cells. Among the latter, however, there is also considerable diversity of form and size.

With the exception of the articular variety, cartilage is invested by a thin, but tough firm fibrous membrane called the *perichondrium*. On the surface of the articular cartilage of the fœtus, the perichondrium is represented by a film of epithelium; but this is gradually worn away up to the margin of the articular surfaces, when by use the parts begin to suffer friction.

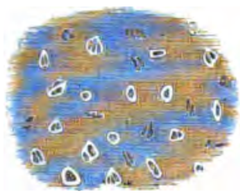
A. *Cellular* or parenchymatous cartilage may be readily obtained from the external ear of rats, mice, or other small mammals. It is composed almost entirely of cells (hence its name), with little or no matrix. The latter, when present, consists of very fine fibres, which twine about the cells in various directions, and enclose them in a kind of network.

The cells are packed very closely together—so much so that it is not easy in all cases to make out the fine fibres often encircling them.

Cellular cartilage is found in the human subject, only in early fœtal life, when it constitutes the Chorda dorsalis. (See chapter on Generation.)

B. *Hyaline cartilage* is met with largely in the human body; —investing the articular ends of bones, and forming the costal cartilages, the nasal and those of the larynx, with the exception of the epiglottis and cornicula laryngis. The cartilages of the trachea and bronchi are also hyaline. Like other cartilages it is composed of cells imbedded in a matrix.

Fig. 34.*



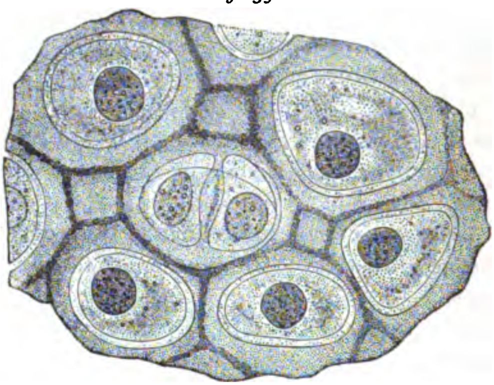
The cells which contain a nucleus with nucleoli, are irregular in shape, and generally grouped together in patches (fig. 34). The patches are of various shapes and sizes, and placed at unequal distances apart. They generally appear flattened near the free surface of the mass of cartilage in which they are placed,

* Fig. 34. Hyaline cartilage.

and more or less perpendicular to the surface in the more-deeply seated portions.

The matrix of hyaline cartilage may have a dimly granular appearance like that of ground glass, but in man and the higher animals it has no apparent structure. In some cartilages of the frog, however, even when examined in the fresh state, the matrix is seen to be mapped out into polygonal blocks or cell territories, each containing a cell in the centre, and representing what is generally called the capsule of the cartilage cells (fig. 35). Hyaline cartilage in man has really the same struc-

Fig. 35.*



ture, which can be demonstrated by the use of certain reagents. If a piece of human hyaline cartilage be macerated for a long time in dilute acid or in hot water 35°—40° C., the matrix, which previously appeared quite homogeneous, is found to be resolved into a number of concentric lamellæ, like the coats of an onion, arranged round each cell or group of cells. It is thus shown to consist of nothing but a number of large systems of capsules which have become fused with one another.

The cavities in the matrix in which the cells lie are connected together by a series of branching canals, very much resembling those in the cornea: through these canals fluids may make their way into the depths of the tissue.

* Fig. 35. Fresh cartilage from the Triton (A. Rollett).

In the hyaline cartilage of the ribs, the cells are mostly larger than in the articular variety, and there is a tendency to the development of fibres in the matrix. The costal cartilages also frequently become calcified in old age, as also do some of those of the larynx.

Temporary hyaline cartilage closely resembles the ordinary hyaline kind; the cells, however, are not grouped together after the fashion just described, but are more uniformly distributed throughout the matrix.

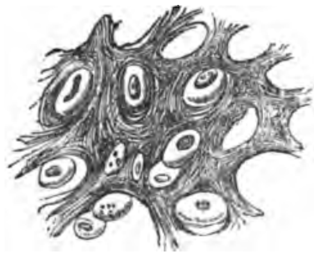
Articular hyaline cartilage is reckoned among the so-called *non-vascular* structures, no blood-vessels being supplied directly to its own substance; it is nourished by those of the bone beneath. When hyaline cartilage is in thicker masses, as in the case of the cartilages of the ribs, a few blood-vessels traverse its substance. The distinction, however, between all so-called *vascular* and *non-vascular* parts, is at the best a very artificial one. (See chapter on Nutrition.)

Nerves are probably not supplied to any variety of cartilage.

C. *Fibrous* cartilage, as before mentioned, occurs under two chief forms, (*a*), the *yellow*, and (*b*) the *white*, fibro-cartilage.

(*a*.) *Yellow fibro-cartilage* is found in the external ear, in the epiglottis and cornicula laryngis, and in the eyelid.

Fig. 36.*



The cells are rounded or oval, with well-marked nuclei and nucleoli (fig. 36). The matrix in which they are seated is composed almost entirely of fine elastic fibres, which form an intricate interlacement about the cells, and in their general characters are allied to the yellow variety of fibrous tissue: a small and variable quantity of hyaline intercellular substance is also usually present.

(*b*.) *White* fibro-cartilage, which is much more widely distributed throughout the body than the foregoing kind, is com-

* Fig. 36. Section of the Epiglottis (Baly). × 380.

posed, like it, of cells and a matrix; the latter, however, being made up almost entirely of fibres closely resembling those of white fibrous tissue (fig. 37).

*Fig. 37.**

In this kind of fibro-cartilage it is not unusual to find a great part of its mass composed almost exclusively of fibres, and deriving the name of cartilage only from the fact that in another portion, continuous with it, cartilage cells may be pretty freely distributed.

The different situations in which white fibro-cartilage is formed have given rise to the following classification:—

1. *Inter-articular* fibro-cartilage, *e.g.*, the semilunar cartilages of the knee-joint.

2. *Circumferential* or marginal, as on the edges of the acetabulum and glenoid cavity.

3. *Connecting*, *e.g.*, the inter-vertebral fibro-cartilages.

4. Fibro-cartilage is found in the sheaths of tendons and sometimes in their substance. In the latter situation, the nodule of fibro-cartilage is called a *sesamoid* fibro-cartilage, of which a specimen may be found in the tendon of the tibialis posticus, in the sole of the foot, and usually in the neighbouring tendon of the peroneus longus.

The *uses* of cartilage are the following:—in the joints to form smooth surfaces, reducing friction to a minimum, and to act as a *buffer* in shocks; to bind bones together, yet to allow a certain degree of movement, as between the vertebræ; to form a firm framework and protection, yet without undue stiffness or weight, as in the pinna, larynx and chest walls; to deepen joint cavities, as in the acetabulum, yet not so as to restrict the movements of the bones; to be, where such qualities are required, firm, tough, flexible, elastic, and strong.

Development of cartilage. It is developed out of an embryonal tissue, consisting of cells with a very small quantity of intercellular substance; the cells multiply by fission within the cell-capsules (fig. 5); while the capsule of the parent cell becomes gradually fused with the surrounding intercellular substance: a

* Fig. 37. White fibro-cartilage.

repetition of this process in the young cells causes a rapid growth of the cartilage by the multiplication of its cellular elements and the corresponding increase in its matrix.

Bones and Teeth.

Bone is composed of earthy and animal matter in the proportion of about 67 per cent. of the former to 33 per cent. of the latter. The earthy matter is composed chiefly of calcium phosphate, but besides there is a small quantity, about 11 of the 67 per cent., of carbonate and fluoride of calcium, and magnesium phosphate.

The animal matter is resolved into gelatin by boiling.

The earthy and animal constituents of bone are so intimately blended and incorporated the one with the other, that it is only by chemical action, as, for instance, by heat in one case, and by the action of acids in another, that they can be separated. Their close union, too, is further shown by the fact that when by acids the earthy matter is dissolved out, or, on the other hand, when the animal part is burnt out, the general shape of the bone is alike preserved.

The proportion between these two constituents of bone, varies in different bones in the same individual, and in the same bone at different ages. Thus, the petrous portion of the temporal bone contains about the largest, and the sternum and scapula about the smallest proportion of earthy or inorganic matter: while the comparatively flexible bones of a child contain a much smaller proportion of earthy matter than the relatively brittle bones of the old man.

To the naked eye there appear two kinds of structure in different bones, and in different parts of the same bone, namely, the *dense* or *compact*, and the *cancellous* tissue.

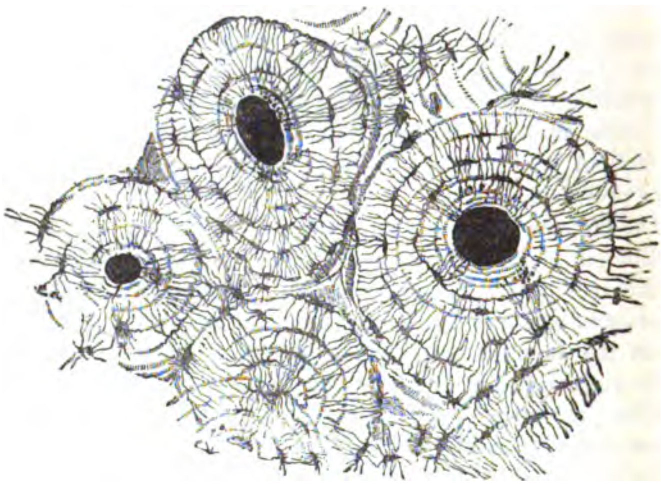
Thus, in making a longitudinal section of a long bone, as the humerus or femur, the articular extremities are found capped on their surface by a thin shell of compact bone, while their interior is made up of the spongy or *cancellous* tissue. The *shaft*, on the other hand, is formed almost entirely of a thick layer of the *compact* bone, and this surrounds a central canal, the

medullary cavity—so called from its containing the *medulla* or marrow (p. 78).

In the flat bones, as the parietal bone, or the scapula, one layer of the cancellous structure lies between two layers of the compact tissue, and in the short and irregular bones, as those of the *carpus* and *tarsus,* the cancellous tissue alone fills the interior, while a thin shell of compact bone forms the outside. The spaces in the cancellous tissue are filled by a species of marrow, which differs considerably from that of the shaft of the long bones. It is more fluid, and of a reddish colour, and contains very few fat cells.

The surfaces of bones, except the parts covered with articular cartilage, are clothed by a tough, fibrous membrane, the *perios-*

Fig. 38.*



teum : and it is from the blood-vessels which are distributed first in this membrane, that the bones, especially their more compact tissue, are in great part supplied with nourishment,—minute

* Fig. 38. Transverse section of compact tissue (of humerus). Three of the Haversian canals are seen, with their concentric rings; also the corpuscles or lacunæ, with the canaliculi extending from them across the direction of the lamellæ. The Haversian apertures had got filled with débris in grinding down the section, and therefore appear black in the figure, which represents the object as viewed with transmitted light. × 150 (Sharpey).

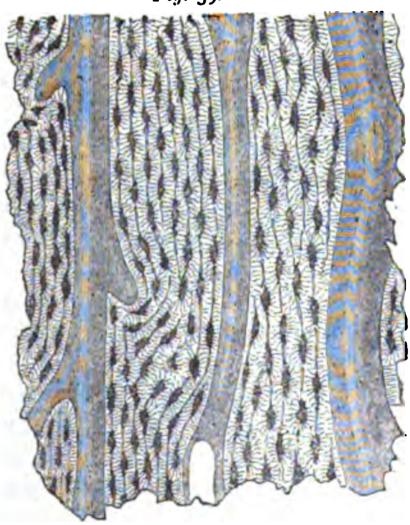
branches from the periosteal vessels entering the little foramina on the surface of the bone, and finding their way to the Haversian canals, to be immediately described. The long bones are supplied also by a proper nutrient artery, which, entering at some part of the shaft so as to reach the medullary canal, breaks up into branches for the supply of the marrow, from which again small vessels are distributed to the interior of the bone.

Other small blood-vessels pierce the articular extremities for the supply of the cancellous tissue.

Notwithstanding the differences of arrangement just mentioned, the structure of all bone is found, under the microscope to be essentially the same.

Examined with a rather high power its substance is found to contain a multitude of little irregular spaces, approximately fusiform in shape, called lacunæ, with very minute canals or canaliculi, as they are termed, leading from them, and anastomosing with similar little prolongations from other lacunæ (fig. 38). In very thin layers of bone, no other canals than these may be visible; but on making a transverse section of the compact tissue, *e.g.*, of a long bone, as the humerus or ulna, the arrangement shown in fig. 38 can be seen.

Fig. 39.



The bone seems mapped out into small circular districts, at or about the centre of each of which is a hole, and around this an appearance as of concentric layers—the *lacunæ* and *canaliculi* following the same con-

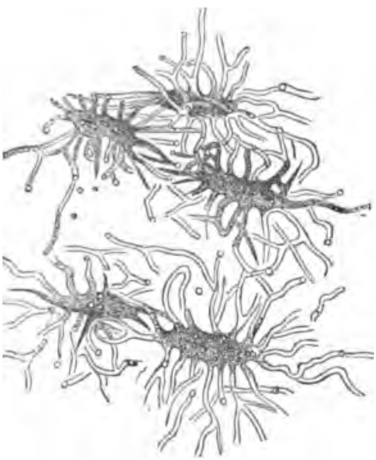
* Fig. 39. Longitudinal section of human ulna, showing Haversian canals, lacunæ, and canaliculi (Rollett).

centric plan of distribution around the small hole in the centre, with which, indeed, they communicate.

On making a longitudinal section, the central holes are found to be simply the cut extremities of small canals which run lengthwise through the bone, anastomosing with each other by lateral branches (fig. 39), and are called Haversian canals, after the name of the physician, Clopton Havers, who first accurately described them. The Haversian canals, the average diameter of which is $\frac{1}{500}$ of an inch, contain blood-vessels, and by means of them, blood is conveyed to all, even the densest parts of the bone; the minute canaliculi and lacunæ absorbing nutrient matter from the Haversian blood-vessels, and conveying it still more intimately to the very substance of the bone which they traverse.

The blood-vessels enter the Haversian canals both from without, by traversing the small holes which exist on the surface of all bones beneath the periosteum, and from within by means of small channels, which extend from the medullary cavity, or from the cancellous tissue.

Fig. 40.*



According to Todd and Bowman, the arteries and veins usually occupy separate canals, and the veins, which are the larger, often present, at irregular intervals, small pouchlike dilatations.

The *lacunæ* are occupied by branched cells (bone-cells, or bone-corpuscles), (fig. 40), which very closely resemble the ordinary branched connective tissue corpuscles; each of these little masses of protoplasm ministering to the nutrition of the bone immediately

* Fig. 40. Bone corpuscles with their processes as seen in a thin section of human bone (Rollett).

surrounding it, and one lacunar corpuscle communicating with another, and with its surrounding district, and with the blood-vessels of the Haversian canals, by means of the minute streams of fluid nutrient matter which occupy the canaliculi.

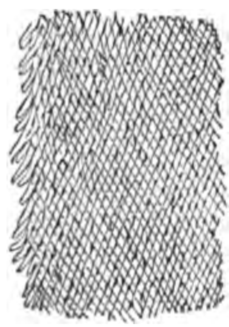
In the shaft of a long bone two distinct sets of lamellæ can be clearly recognized.

(1.) *General* or fundamental lamellæ: which are most easily traceable just beneath the periosteum, and around the medullary cavity, forming around the latter a series of concentric rings. At a distance from the medullary and periosteal surfaces (in the deeper portions of the bone) they are more or less interrupted by

(2.) *Special* or Haversian lamellæ, which surround the Haversian canals to the number of six to eighteen around each.

The ultimate structure of the *lamellæ* appears to be reticular. If a thin film be peeled off the surface of a bone from which the earthy matter has been removed by acid, and examined with a high power of the microscope, it will be found composed, according to Sharpey, of a finely reticular structure, formed apparently of very slender fibres decussating obliquely, but coalescing at the points of intersection, as if here the fibres were fused rather than woven together (fig. 41).

Fig. 41.*



In many places these reticular lamellæ are perforated by tapering fibres, resembling in character the ordinary white or rarely the elastic fibrous tissue, which bolt the neighbouring lamellæ together, and may be drawn out when the latter are torn asunder (fig. 42).

Development of bone.—From the point of view of their development, all bones may be subdivided into two classes.

* Fig. 41. Thin layer peeled off from a softened bone. This figure, which is intended to represent the reticular structure of a lamella, gives a better idea of the object when held rather farther off than usual from the eye. × 400 (Sharpey).

(*a.*) Those whose form, previous to ossification, is laid down in hyaline cartilage, *e.g.*, humerus, femur, &c.

(*b.*) Those which are not preformed in cartilage, but are ossified directly in membrane, *e.g.*, the bones forming the vault of the skull, parietal, frontal, &c.

The true process of ossification is really the same in both, only in (*a*) it is preceded by a calcification of the cartilage matrix. The former method may be considered first.

(*a.*) *Ossification in Cartilage.*—If a section be taken through a carti-

Fig. 42.*

Fig. 43.†

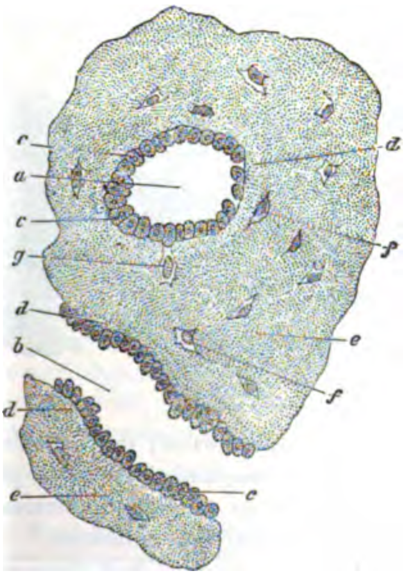
lage in which calcification is going on (fig. 43), as, *e.g.*, the extremity of the shaft of a long bone, the cartilage-cells are seen

* Fig. 42. Lamellæ torn off from a decalcified human parietal bone at some depth from the surface. *a*, a lamella, showing reticular fibres; *b*, *b*, darker part, where several lamellæ are superposed; *c*, perforating fibres. Apertures through which perforating fibres had passed, are seen especially in the lower part, *a*, *a*, of the figure (Allen Thompson).

† Fig. 43. Longitudinal section of ossifying cartilage from the humerus of a fœtal sheep. Spiculæ of bone are seen extending between the columns of cartilage cells. *c*, cartilage cells. × 140 (Sharpey).

to be collected into regular columns arranged perpendicular to the plane of calcification, the individual cells being flattened from above downwards. Shooting up into the matrix of the cartilage intervening between the columns of cells are seen delicate calcified spiculæ, the calcareous matter being deposited in small granules from the blood-vessels which are arranged in loops perpendicular to the calcifying surface. As the spiculæ shoot further and further up into the cartilage, most of the cartilage-cells disappear; the larger part of the hyaline matrix becoming replaced by calcareous spiculæ, and the process of calcification is thus completed. Between these spiculæ are irregular spaces originally occupied by the cartilage-cells, many of which have now become liquefied and disappeared. These spaces are further enlarged and rendered more irregular by the absorption of the remains of the cartilaginous matrix surrounding the spiculæ.

*Fig. 44.**



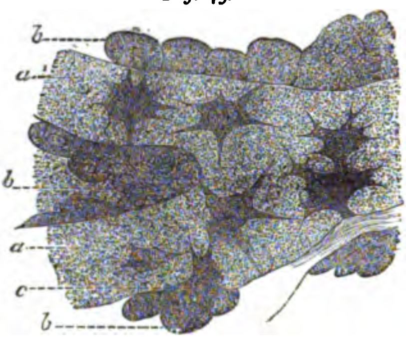
These irregular spaces become lined as by an epithelium, with spheroidal cells (*osteoblasts*), derived partly from the remaining cartilage-cells, but chiefly from ingrowing processes of periosteum (fig. 44). The true process of ossification, as distinct from the preceding

* Fig. 44. Transverse section of femur of a human embryo of about eleven weeks old. *a*, rudimentary Haversian canal in cross section; *b*, in longitudinal section; *c*, osteoblasts; *d*, newly formed osseous substance of a lighter colour; *e*, that of greater age; *f*, lacunæ with their cells; *g*, a cell still united to an osteoblast (Frey).

calcification of the cartilage, consists in the gradual deposition, around this layer of osteoblasts, of a lamella of bone. The individual osteoblasts are imbedded in it and, becoming branched, persist as bone-corpuscles. The inner surface of this lamella is lined by a fresh layer of osteoblasts, and a fresh layer of bone is deposited concentric with the first; this process continuing till the large irregular space is reduced to a small "Haversian canal" (fig. 44).

(*b*.) *Ossification in Membrane.*—The membrane or periosteum, from which such a bone as the parietal is developed consists of two layers—an external *fibrous*, and an internal cellular or *osteogenetic*. The external one consists of ordinary connective tissue, being composed largely of fusiform cells and some fibres; the internal layer consists of rounded cells quite undistinguishable from the osteoblasts above mentioned.

Fig. 45.*



The process of ossification in membrane, as seen, *e.g.*, in the parietal bone (fig. 45), is precisely similar to that which takes place in cartilage, if, as before said, we except the previous calcification; the *osteoblasts* being doubtless derived from the osteogenetic layer of the periosteum.

In all bones ossification commences at one or more points, termed "centres of ossification." The long bones, *e.g.*, femur, humerus, &c., have at least three such points—one for the ossification of the *shaft* or *diaphysis*, and one for each articular extremity or *epiphysis*. Besides these three primary centres which are always present in long bones, various secondary centres may be superadded for the ossification of different *processes*.

* Fig. 45. Osteoblasts from the parietal bone of a human embryo, thirteen weeks old. *a*, bony septa with the cells of the lacunæ; *b*, layers of osteoblasts; *c*, the latter in transition to bone corpuscles (Gegenbaur).

Such bones increase in length by the advance of the process of ossification into the cartilage intermediate between the diaphysis and epiphysis. The increase in length indeed is due entirely to growth at the two ends of the *shaft*. This is proved by inserting two pins into the shaft of a growing bone: after some time their distance apart will be found to be unaltered though the bone has gradually increased in length, the growth having taken place beyond and not between them. If now one pin be placed in the shaft, and the other in an epiphysis of a growing bone, their distance apart will increase as the bone grows in length.

Thus it is that if the epiphyses with the intermediate cartilage be removed from a young bone, growth in length is no longer possible.

Increase in thickness in the shaft of a long bone, occurs by the deposition of successive layers beneath the periosteum.

If a thin metal plate be inserted beneath the periosteum of a growing bone, it will soon be covered by osseous deposit, but if it be put between the fibrous and osteogenetic layers, it will never become enveloped in bone, for all the bone is formed beneath the latter. Side by side with the increase in length and thickness above-mentioned, there goes on a hollowing out of the shaft of long bones by absorption, producing in the mature bone a large cavity—medullary cavity. This cavity in the long bone of the adult is much larger than the cartilaginous mould of the bone in the fœtus, and thus it is obvious that not a trace of the original embyronic cartilaginous mould can be present in the adult bone.

Other varieties of connective tissue may become ossified, *e.g.*, the tendons in some birds.

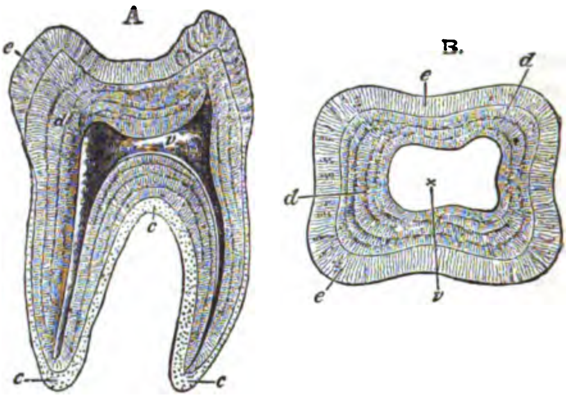
Functions of bones.—Bones form the framework of the body; for this they are fitted by their hardness and solidity together with their comparative lightness; they serve both to protect internal organs in the trunk and skull, and as levers worked by muscles in the limbs; notwithstanding their hardness they possess a considerable degree of elasticity, which often saves them from fractures.

Teeth.—A tooth is generally described as possessing a *crown*, *neck*, and *fang* or *fangs*.

The *crown* is the portion which projects beyond the level of the gum. The *neck* is that constricted portion just below the crown which is embraced by the free edges of the gum, and the *fang* includes all below this.

On making a longitudinal section through the centre of a tooth (figs. 46, 47), it is found to be principally composed of a

Fig. 46.*



hard matter, *dentine* or ivory; while in the centre this dentine is hollowed out into a cavity resembling in general shape the outline of the tooth, and called the *pulp-cavity*, from its containing a very vascular and sensitive little mass, composed of connective-tissue, blood-vessels, and nerves, which is called the *tooth-pulp*.

The blood-vessels and nerves enter the pulp through a small opening at the extremity of the fang.

Capping that part of the dentine which projects beyond the level of the gum, is a layer of very hard calcareous matter, the *enamel*; while sheathing the portion of dentine which is beneath the level of the gum, is a layer of true bone, called the *cement* or *crusta petrosa*.

At the neck of the tooth, where the enamel and cement come

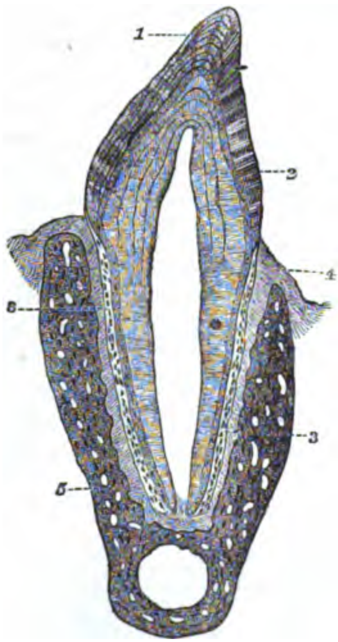
---

* Fig. 46. A. Longitudinal section of a human molar tooth; *c*, cement; *d*, dentine; *e*, enamel; *v*, pulp cavity (Owen).

B. Transverse section. The letters indicate the same as in A.

into contact, each is reduced to an exceedingly thin layer. The covering of enamel becomes thicker as we approach the crown, and the cement as we approach the lower end or apex of the fang.

Fig. 47.*



Dentine or ivory in chemical composition closely resembles bone. It contains, however, rather less animal matter; the proportion in hundred parts being about twenty-eight *animal* to seventy-two of *earthy*. The former, like the animal matter of bone, may be resolved into gelatin by boiling. The earthy matter is made up chiefly of calcium phosphate, with a small portion of the carbonate, and traces of fluoride of calcium and phosphate of magnesium.

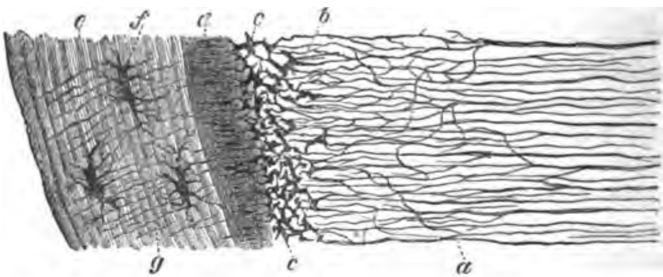
Under the microscope dentine is seen to be finely channelled by a multitude of delicate tubes, which, by their inner ends, communicate with the pulp-cavity, and by their outer extremities come into contact with the under part of the enamel and cement and sometimes even penetrate them for a greater or less distance (fig. 48).

In their course from the pulp-cavity to the surface of the dentine, the minute tubes form gentle and nearly parallel curves and divide and subdivide dichotomously, but without much lessening their calibre until they are approaching their peripheral termination.

* Fig. 47. Premolar tooth of cat *in situ*. Vertical section. 1. Enamel with decussating and parallel striæ. 2. Dentine with Schreger's lines. 3. Cement. 4. Periosteum of the alveolus. 5. Inferior maxillary bone (Waldeyer).

From their sides proceed other exceedingly minute secondary canals, which extend into the dentine between the tubules, and anastomose with each other. The tubules of the dentine, the average diameter of which at their inner and larger extremity is $\frac{1}{4500}$ of an inch, contain fine prolongations from the tooth-pulp, which give the dentine a certain faint sensitiveness under ordinary circumstances, and without doubt, have to do also with its nutrition. These prolongations from the tooth-pulp are really processes of the dentine-cells or *odontoblasts*, which are branched cells lining the pulp-cavity; the relation of these processes to the tubules in which they lie, is precisely similar to that of the processes of the bone-corpuscles to the canaliculi of bone. The outer portion of the dentine underlying both the cement and enamel, forms a more or less distinct layer termed the *granular* or *interglobular* layer. It is characterised by the presence of a number of minute cell-like cavities, much more closely packed than the lacunæ in the cement, and communicating with one another, and with the ends of the dentine-tubes (fig. 48).

Fig. 48.*



The *enamel* which is by far the hardest portion of a tooth, is composed, chemically, of the same elements that enter into the composition of dentine and bone. Its animal matter, however, amounts only to about 2 or 3 per cent. It contains a larger

* Fig. 48. Section of a portion of the dentine and cement from the middle of the root of an incisor tooth. *a*, dental tubuli ramifying and terminating, some of them in the interglobular spaces *b* and *c*, which somewhat resemble bone lacunæ; *d*, inner layer of the cement with numerous closely set canal liculi; *e*, outer layer of cement; *f*, lacunæ; *g*, canaliculi. × 350. (Kölliker.)

proportion of inorganic matter, and is harder than any other tissue in the body.

Examined under the microscope, enamel is found composed of fine hexagonal fibres (figs. 49, 50) $\frac{1}{5000}$ of an inch in diameter,

Fig. 49.*

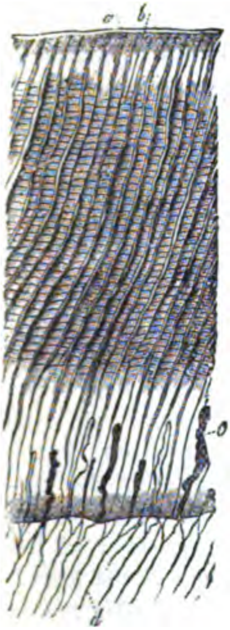
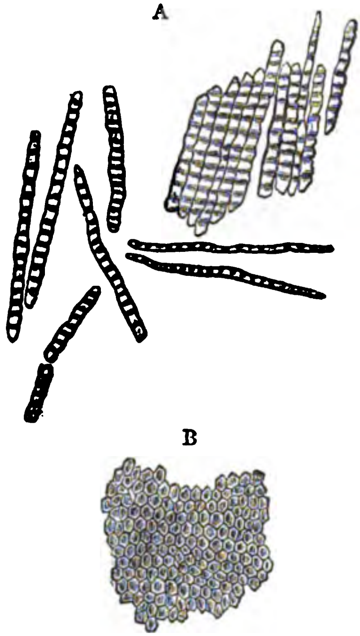


Fig. 50.†



which are set on end on the surface of the dentine, and fit into corresponding depressions in the same.

They radiate in such a manner from the dentine that at the top of the tooth they are more or less vertical, while towards the sides they tend to the horizontal direction. Like the dentine-

* Fig. 49. Thin section of the enamel and a part of the dentine. *a*, cuticular pellicle of the enamel; *b*, enamel fibres, or columns with fissures between them and cross striæ; *c*, larger cavities in the enamel, communicating with the extremities of some of the tubuli (*d*). × 350. (Kölliker.)

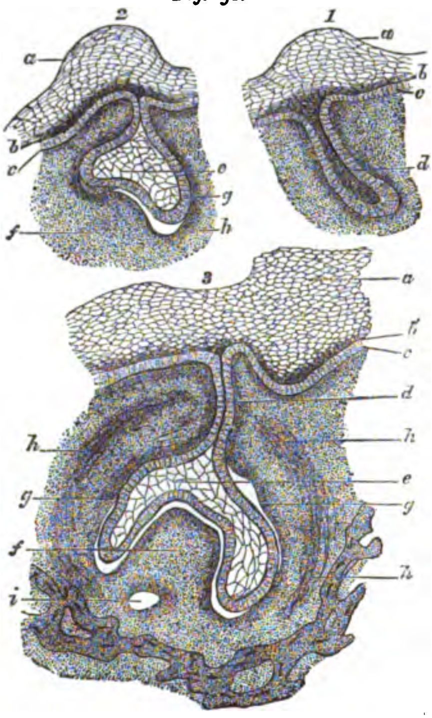
† Fig. 50. Enamel fibres. A, fragments and single fibres of the enamel, isolated by the action of hydrochloric acid. B, surface of a small fragment of enamel, showing the hexagonal ends of the fibres. × 350. (Kölliker.)

tubules, they are not straight, but disposed in wavy and parallel curves. The fibres are marked by transverse lines, and are mostly solid, but some of them contain a very minute canal.

The enamel itself is coated on the outside by a very thin calcified membrane, sometimes termed the *cuticle* of the enamel.

The *crusta petrosa*, or, *cement*, is composed of true bone, and in it are lacunæ and canaliculi which sometimes communicate with the outer finely branched ends of the dentine tubules. Its laminæ are as it were bolted together by perforating fibres like those of ordinary bone (see fig. 42), but it differs in not possessing Haversian canals.

Fig. 51.



Development of teeth.

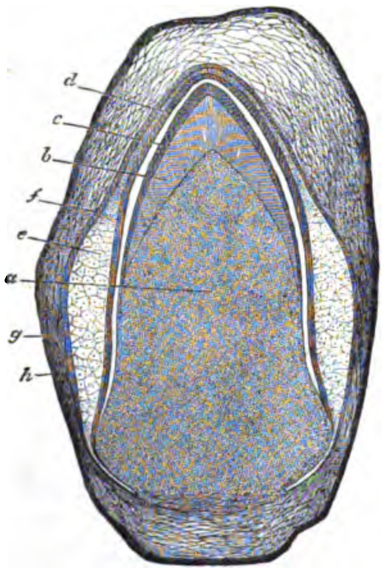
The first step in the development of the teeth, consists in a thickening of the epithelium which covers the free border of the jaw, and in the formation of a shallow groove in the subjacent tissue (primitive dental groove of Goodsir) in which it is contained

The deeper layer of this epithelium begins

Fig. 51. Development of the teeth. Vertical transverse sections of upper jaw. 1, 2. From a small embryo; *a*, dental ridge; *b*, younger layers of epithelium; *c*, the deepest; *d*, enamel germ; *e*, enamel organ; *f*, dental germ; *g*, inner; and *h*, outer layer of the growing tooth sac. 3. From an older embryo; *d*, the style of the enamel organ; *i*, blood-vessel severed; *k*, bony substance. The remaining letters as in 1 and 2 (Thiersch).

to grow down into the substance of the mucous membrane, forming an ingrowing process which is met and indented by an upwardly growing papilla : the papilla, in its growth towards the free surface, indents this epithelial process (fig. 51) more and more till the latter forms, as it were, a cap for the dental papilla (enamel organ), consisting of two layers of cylindrical epithelium, which are in close apposition towards the apex of the papilla, but elsewhere are separated by a mass of loosely arranged stellate cells. The pedicle or stalk of cells by which the "enamel organ" communicates with the free surface gradually disappears : and the embryonic tooth becomes completely enveloped in its dental sac (see fig. 52). A glance at the accompanying figures (51 and 52) will render all these points clear.

*Fig. 52.**



It is to be observed that the papilla and the surrounding dental sac are both well-supplied with blood-vessels, while the enamel-organ, though now quite separated from the epithelium, shows its epithelial character by the entire absence of vessels.

The papilla gradually becomes moulded into the shape of the crown of the future tooth, while a cap of dentine is slowly deposited on it, increasing in extent by additions to its edges, and in thickness by additions to its interior.

* Fig. 52. Vertical transverse section of the dental sac, pulp, &c., of a kitten. × 14. (Thiersch.) *a*, dental papilla or pulp ; *b*, the cap of dentine formed upon the summit ; *c*, its covering of enamel ; *d*, inner layer of epithelium of the enamel organ ; *e*, gelatinous tissue ; *f*, outer epithelial layer of the enamel organ ; *g*, inner layer, and *h*, outer layer of dental sac.

The substance of the papilla undergoes a corresponding decrease, and its remains finally persist as the pulp of the mature tooth.

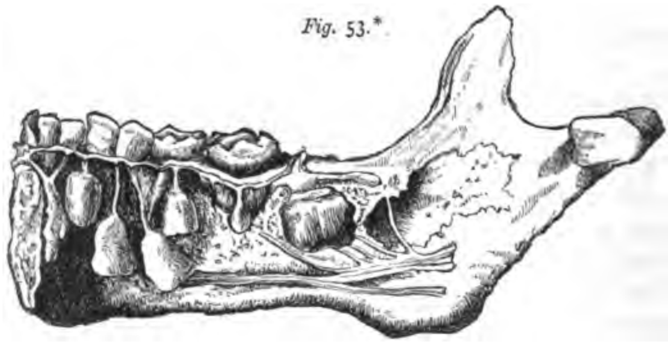
At the same time that layer of the enamel organ which is in immediate contact with the dentinal cap, becomes transformed into enamel by the direct calcification of the long cylindrical epithelial cells of which it was originally composed: the layers of the enamel organ external to this remain as the cuticle above mentioned (sometimes termed Nasmyth's membrane).

In this manner the first set of teeth, or the milk-teeth, are formed; and each tooth, by degrees developing, presses at length on the wall of the sac enclosing it, and causing its absorption, is *cut*, to use a familiar phrase.

As the tooth grows upwards the fang is gradually calcified, and the cement is deposited on it from the inner layer of the tooth-sac.

The *temporary* or *milk-teeth*, have only a very limited term of existence: this is due to the growth of the permanent teeth, which push their way up from beneath, absorbing in their

Fig. 53.*



* Fig. 53. Part of the lower jaw of a child of three or four years old, showing the relations of the temporary and permanent teeth. The specimen contains all the milk-teeth of the right side, together with the incisors of the left; the inner plate of the jaw has been removed, so as to expose the sacs of all the permanent teeth of the right side, except the eighth or wisdom tooth, which is not yet formed. The large sac near the ramus of the jaw is that of the first permanent molar, and above and behind it is the commencing rudiment of the second molar. (Quain.)

progress the whole of the fang of each milk-tooth, and leaving at length only the crown as a mere shell, which is shed to make way for the eruption of the permanent teeth (fig. 53).

The temporary teeth are ten in each jaw, mamely, four *incisors*, two *canines*, and four *molars*, and are replaced by ten permanent teeth, each of which is developed from a small sac set by, so to speak, from the sac of the temporary tooth which precedes it, and called the *cavity of reserve*.

The number of permanent teeth is, however, increased to sixteen, by the development of three others on each side of the jaw after much the same fashion as that by which the milk-teeth were themselves formed.

The beginning of the development of the permanent teeth of course takes place long before the *cutting* of those which they are to succeed; one of the first acts of the newly-formed little dental sac of a milk-tooth being to set aside a portion of itself as the germ of its successor.

The following formula shows, at a glance, the comparative arrangement and number of the temporary and permanent teeth:—

		MO.	CA.	IN.	CA.	MO.		
Temporary Teeth......	Upper	2	1	4	1	2	=10	=20
	Lower	2	1	4	1	2	=10	

		MO.	BI.	CA.	IN.	CA.	BI.	MO.		
Permanent Teeth......	Upper	3	2	1	4	1	2	3	=16	=32
	Lower	3	2	1	4	1	2	3	=16	

From this formula it will be seen that the two bicuspid teeth in the adult are the successors of the two molars in the child. They differ from them, however, in some respects, the *temporary* molars having a stronger likeness to the *permanent* than to their immediate descendants, the so-called bicuspids.

The temporary incisors and canines differ from their successors but little except in their smaller size.

The following tables show the average times of eruption of the Temporary and Permanent teeth. In both cases, the eruption of any given tooth of the lower jaw precedes, as a rule, that of the corresponding tooth of the upper.

Temporary or Milk Teeth.

The figures indicate in *months* the age at which each tooth appears.

MOLARS.	CANINES.	INCISORS.	CANINES.	MOLARS.
24 12	18	9 7 7 9	18	12 24

Permanent Teeth.

The age at which each tooth is cut is indicated in this table in *years*.

MOLARS.	BICUSPID.	CANINES.	INCISORS.	CANINES.	BICUSPID.	MOLARS.
17 to 25, 12 to 13, 6	10 9	11 to 12	8 7 7 8	11 to 12	9 10	6, 12 to 13, 17 to 25

The times of eruption put down in the above tables are only approximate: the limits of variation being tolerably wide. Some children may cut their first teeth before the age of six months and others not till nearly the twelfth month. In nearly all cases the two central incisors of the lower jaw are cut first; these being succeeded after a short interval by the four incisors of the upper jaw; next follow the lateral incisors of the lower jaw, and so on as indicated in the table till the completion of the milk dentition at about the age of two years.

The milk-teeth usually come through in batches, each period of eruption being succeeded by one of quiescence lasting sometimes several months. The milk-teeth are in use from the age of two up to five and a half years: at about this age the first permanent molars (four in number) make their appearance *behind* the milk molars, and for a short time the child has four permanent and twenty temporary teeth in position at once.

It is worthy of note that from the age of five years to the shedding of the first milk-tooth the child has no fewer than forty-eight teeth, twenty milk-teeth and twenty-eight calcified germs of permanent teeth (all in fact except the four wisdom teeth).

CHAPTER VI.

THE BLOOD.

As blood flows from the living body, it is seen to be a thickish heavy fluid, of a bright scarlet colour when it comes from an artery; deep purple or nearly black when flowing from a vein. Although to the naked eye, however, it seems uniformly tinted, it is found by the microscope to be really a colourless fluid, containing minute coloured cells or corpuscles; and these cells, which are red, when seen *en masse*, are the real source of the colour which seems to the naked eye to belong to every part of the blood alike. The colourless fluid portion of the blood is termed *liquor sanguinis*, or *plasma*; the coloured cells are termed *blood-cells*, or *blood-corpuscles*.

The blood is, even in very thin layers, opaque, on account of the different refractive powers of the corpuscles and the plasma in which they are suspended; but it assumes a lake tint, and becomes transparent on the employment of means by which the colouring matter is dissolved out of the corpuscles by the plasma (p. 116). Its specific gravity at 60° F. is on an average 1055; the extremes consistent with health being 1050 and 1059. It has a faint alkaline re-action. Its temperature is generally about 100° F.; but this is not the same in all parts of the body. Thus, while the stream is slightly warmed by passing through the muscles, nerve-centres, and glands, most notably the liver, it is slightly cooled on traversing the capillaries of the skin. (Bernard.)

The odour of blood is easily perceived in the watery vapour which rises from blood just drawn: and it may also be set free, afterwards, by adding to the blood a mixture of equal parts of sulphuric acid and water. It is said not to be difficult to tell, by the likeness of the odour to that of the body, the species of domestic animal from which any specimen of blood has been

taken. The strong odour of the pig or cat, and the peculiar milky smell of the cow, are especially easy to be detected. (Barruel.)

Quantity of Blood.

Only an imperfect indication of the whole quantity of blood in the body is afforded by measurement of that which escapes when an animal is rapidly bled to death, inasmuch as a certain amount always remains in the blood-vessels. In cases of less rapid bleeding, on the other hand, when life is more prolonged, and when, therefore, sufficient time elapses before death to allow some absorption into the circulating current of the fluids of the body (p. 122), the whole quantity of blood that escapes may be greater than the whole average amount naturally present in the vessels.

Various means have been devised for obtaining a more accurate estimate than that which results from merely bleeding animals to death.

Welcker's method is the following. An animal is rapidly bled to death, and the blood which escapes is collected and measured. The blood remaining in the smaller vessels is then removed by the injection of water through them, and the mixture of blood and water thus obtained, is also collected. The animal is then finely minced, and infused in water, and the infusion is mixed with the combined blood and water previously obtained. Some of this fluid is then brushed on a white ground, and the colour compared with that of mixtures of blood and water whose proportions have been previously determined by measurement. In this way the materials are obtained for a fairly exact estimate of the quantity of blood actually existing in the body of the animal experimented on.

Another method (that of Vierordt) consists in estimating the amount of blood expelled from the ventricle, at each beat of the heart, and multiplying this quantity by the number of beats necessary for completing the "round" of the circulation. This method is ingenious, but open to various objections, the most conclusive being the uncertainty of all the premisses on which the conclusion is founded.

Other methods depend on the results of injecting a known quantity of water (Valentin) or of saline matters (Blake) into the blood-vessels; the calculation being founded, in the first case, on the diminution of the specific gravity which ensues, and in the other, on the quantity of the salt found diffused in a certain measured amount of the blood abstracted for experiment.

A nearly correct estimate was probably made by Weber and Lehmann, from the following data. A criminal was weighed before and after decapitation; the difference in the weight representing, of course, the quantity of blood which escaped. The blood-vessels of the head and trunk were then washed out by the injection of water, until the fluid which escaped had only

a pale red or straw colour. This fluid was then also weighed; and the amount of blood which it represented was calculated, by comparing the proportion of solid matter contained in it, with that of the first blood which escaped on decapitation. Two experiments of this kind gave precisely similar results.

The most reliable of the various means for estimating the quantity of blood in the body yield as nearly similar results as can be expected, when the sources of error unavoidably present in all, are taken into consideration; and it may be stated that in man, the weight of the whole quantity of blood, compared with that of the body, is from about 1 to 8, to 1 to 10.

It must be remembered, however, that the whole quantity of blood varies, even in the same animal, very considerably, in correspondence with the different amounts of food and drink, which may have been recently taken in, and the equally varying quantity of matter given out. Bernard found by experiment, that the quantity of blood obtainable from a fasting animal is scarcely more than a half of that which is present soon after a full meal. The estimate above given must therefore be taken to represent only an approximate average.

Coagulation of the Blood.

In a very few minutes after removal from the living body, blood becomes semi-solid and jelly-like by the formation throughout its whole substance of what is called the *crassamentum* or *clot.*

The clot thus formed has at first the same volume and appearance as the fluid blood, and, like it, looks quite uniform; the only change seems to be, that the blood which was fluid is now solid. But presently, drops of transparent yellowish fluid begin to ooze from the surface of the solid clot; and these gradually collecting, first on its upper surface, and then all around it, the clot, diminished in size, but firmer than it was before, floats in a quantity of yellowish fluid, which is named *serum*, the quantity of which may continually increase on account of its being gradually squeezed out of the meshes of the clot in the course of its contraction, for from twenty-four to forty-eight hours after coagulation.

Blood clot is composed of red corpuscles, held together as a solid mass, in the meshes of a substance termed *fibrin;* the latter being formed, at the moment of coagulation, in the *liquor sanguinis.* A rough analysis of the blood is thus spontaneously made.

Blood.

Liq. Sanguinis or Plasma. Corpuscles.

Serum. Fibrin.

Clot (containing also more or less serum).

That the fibrin is formed in the *plasma* may be proved by employing means by which, before coagulation, the plasma and corpuscles are separated, the one from the other. In the case of the blood of animals, as the frog, which have large corpuscles, this separation can be effected simply by filtration; the colourless *liquor sanguinis* passing through and spontaneously coagulating as a colourless jelly, while the corpuscles remain on the filter.

The same thing can be effected in the blood of mammalia by exposing it to cold of about 32° F. By this means, coagulation is prevented; and the corpuscles, having now time to subside, leave the clear supernatant plasma, which spontaneously forms a colourless clot as soon as the temperature is allowed to rise.

Under ordinary circumstances, however, coagulation occurs before the red corpuscles have had time to subside; and thus, from their being entangled in the meshes of the fibrin, the clot is of a deep dark red colour throughout,—somewhat darker, it may be, at the most dependent part, from accumulation of red cells, but not to any very marked degree. If, however, from any cause, the red corpuscles sink more quickly than usual, or the fibrin contracts more slowly, then, in either of these cases, the red corpuscles may be observed, while the blood is yet fluid, to sink below its surface; and the layer beneath which they have sunk, and which has usually an opaline or greyish white tint, will coagulate without them, and form a colourless or buff-coloured clot consisting of fibrin alone, or of fibrin with entangled white corpuscles; for the white corpuscles, being very light, tend

upwards towards the surface of the fluid. The layer of clot which is thus formed rests on the top of a coloured clot of ordinary character, *i.e.*, of one in which the coagulating fibrin has entangled the red corpuscles while they were sinking: and, thus placed, it constitutes what has been called a *buffy coat.*

When a buffy coat is formed in the manner just described, it commonly contracts more than the rest of the clot, on account of the absence of red corpuscles from its meshes, and contraction being less interfered with by adhesion to the interior of the containing vessel in the vertical than the horizontal direction (Burdon-Sanderson), a *cupped* appearance is produced on the top of the clot.

In certain conditions of the system, and especially when there exists some local inflammation, this buffed and cupped condition of the clot is well marked, because the tendency of the red corpuscles to form rouleaux (see p. 115) is much exaggerated in inflammatory blood; and their rate of sinking increases with their aggregation. Inflammatory blood coagulates also less rapidly, although more firmly, than healthy blood.

Although the appearance just described is commonly the result of a condition of the blood in which there is an increase in the quantity of fibrin, it need not of necessity be so. For a very different state of the blood, such as that which exists in chlorosis, may give rise to the same appearance ; but in this case the pale layer is due to a relatively smaller amount of red corpuscles.

It is a curious fact that in the case of the horse, the buffed and cupped appearance of the blood is a natural phenomenon, and has no connection with those conditions of disease under which alone it appears in man.

Fibrin does not exist, as fibrin, in liquid blood. It is always formed, in the act of coagulation, by the union of two albuminous substances, which, by some means yet unknown, exist separately in the blood, as it circulates. These fibrin-forming substances are termed *paraglobulin* (fibrino-plastic substance) and *fibrinogen*.

Experiments made many years ago by Dr. Andrew Buchanan of Glasgow, and confirmed by more recent independent observations of Alexander Schmidt, have led chiefly to this belief.

When blood-serum or blood clot is added to the fluid of hydrocele, or any other serous effusion, it speedily causes coagulation with the production of fibrin. And this phenomenon may occur also on the admixture of serous effusions from different parts of the body, as that of hydrocele with that of ascites, or of either with fluid from the pleural cavity. Other substances also, as muscular or nervous tissue, skin, &c., have been found to excite coagulation in serous fluids.

Thus, fluids which have no tendency to coagulate spontaneously can be made to produce a clot identical with blood-fibrin, by the addition to them of some other albuminous fluids and substances.

Fibrino-plastic matter (paraglobulin) can be obtained as a granular precipitate by passing a current of carbonic acid gas through a mixture of ice-cold plasma and water, or dilute serum. From the former mixture, a second precipitate (fibrinogen) can be obtained by passing carbonic acid gas through the clear liquid left by the subsidence of the paraglobulin, after diluting it with twice its bulk of ice-cold water. Fibrinogen may be obtained also from hydrocele fluid by saturating it with chloride of sodium; while a similar treatment of serum will precipitate paraglobulin.

The fact that the fluid part (plasma) of the blood contains in itself the factors required for the formation of fibrin must not be taken as a proof that the corpuscles have nothing to do under ordinary circumstances with the process of coagulation. The reverse appears to be the case.

Serum to which coloured blood corpuscles, which have been separated by subsidence and decantation from a known quantity of blood, are added, acquires the property of coagulation; and that the colourless corpuscles may have also a large share in the formation of fibrin, may be inferred from several facts. "Vaccine and blister fluid are both coagulable; they contain no coloured blood-corpuscles, but always many colourless corpuscles. If the process of coagulation is watched in either of these liquids under the microscope, it is seen, not merely that it begins from these elements, but that it occurs nowhere in the liquid excepting where they are present. Again, if a ligature is drawn through a vein in which blood is circulating, as, *e.g.*, through the external jugular of a rabbit or guinea-pig, and allowed to remain there

for a time, and then removed and examined microscopically, it is found that the threads of the ligature are crowded, and its surface encrusted with colourless corpuscles. These bodies are held together by fibrin, which appears to grow from their surface into the blood-stream." (Burdon-Sanderson.)

The share, however, taken in ordinary blood-coagulation by the coloured and colourless corpuscles, either comparatively or absolutely, is still unknown.

The immediate cause of the coagulation of the blood, is still a mystery.

Prof. Lister supposes that blood has no natural tendency to clot, but that its coagulation out of the body is due to the action of foreign matter with which it happens to be brought into contact, and, in the body, to conditions of the tissues, which cause them to act towards it like foreign matter.

Another theory (Brücke's) differs from the last, in that while it admits a natural tendency on the part of the blood to coagulation, it supposes that this tendency in the living body is restrained by some inhibitory power resident in the walls of the containing vessels.

Support was once thought to be given to this and like theories by cases of injury, in which blood extravasated in the living body has seemed to remain uncoagulated for weeks, or even months, on account of its contact with living tissues. But the supposed facts have been shown to be without foundation. The blood-like fluid in such cases is not uncoagulated blood, but a mixture of serum and blood-corpuscles, with a certain proportion of clot in various stages of disintegration. (Morrant Baker.)

Conditions affecting Coagulation.

The coagulation of the blood is hastened by the following means :—

1. Moderate warmth,—from about 100° F. to 120° F.

2. *Rest* is favourable to the coagulation of blood. Blood, of which the whole mass is kept in uniform motion, as when a closed vessel completely filled with it is constantly moved, coagulates very slowly and imperfectly.

3. Contact with foreign matter, and especially multiplication of the points of contact. Thus, coagulated fibrin may be quickly

obtained from liquid blood by stirring it with a bundle of small twigs; and even in the living body the blood will coagulate upon rough bodies projecting into the vessels; as, for example, upon threads passed through them, or upon the heart's valves roughened by inflammatory deposits or calcareous accumulations.

4. The free access of air.

5. Coagulation is quicker in shallow than in tall and narrow vessels.

6. The addition of less than twice the bulk of water.

The blood last drawn is said to coagulate more quickly than the first.

The coagulation of the blood is retarded by the following means:—

1. *Cold* retards coagulation; and so long as blood is kept at a temperature below 40° F., it will not coagulate at all. Freezing the blood, of course, prevents its coagulation; yet it will coagulate, though not firmly, if thawed after being frozen; and it will do so, even after it has been frozen for several months. A higher temperature than 120° F. retards coagulation, or, by coagulating the albumen of the serum, prevents it altogether.

2. The addition of water in greater proportion than twice the bulk of the blood.

3. Contact with living tissues, and especially with the interior of a living blood-vessel, retards coagulation.

4. The addition of alkaline and earthy salts in the proportion of 2 or 3 per cent. and upwards. When added in large proportion most of these saline substances prevent coagulation altogether. Coagulation, however, ensues on dilution with water. The time that blood can be thus preserved in a liquid state and coagulated by the addition of water, is quite indefinite.

5. Imperfect aëration,—as in the blood of those who die by asphyxia.

6. In inflammatory states of the system, the blood coagulates more slowly although more firmly.

7. Coagulation is retarded by exclusion of the blood from the air, as by pouring oil on the surface, etc. In vacuo, the blood coagulates quickly; but Prof. Lister thinks that the rapidity of

the process is due to the bubbling which ensues from the escape of gas, and to the blood being thus brought more freely into contact with the containing vessel.

The coagulation of the blood is prevented altogether by the addition of strong acids and caustic alkalies.

It has been believed, and chiefly on the authority of Mr. Hunter, that after certain modes of death, the blood does not coagulate; he enumerates the death by lightning, over-exertion (as in animals hunted to death), blows on the stomach, fits of anger. He says, "I have seen instances of them all." Doubtless he had done so; but the results of such events are not constant. The blood has been often observed coagulated in the bodies of animals killed by lightning or an electric shock; and Mr. Gulliver has published instances in which he found clots in the hearts of hares and stags hunted to death, and of cocks killed in fighting.

Chemical Composition of the Blood.

Average proportions of the constituents of the blood in 1,000 parts:—

Water		784·
Albumen (of serum)		70·
Fibrin		2·2
Red corpuscles (dry)		130·
Fatty matters		1·4
Inorganic Salts:	Chloride of sodium	3·6
	Chloride of potassium	0·35
	Tribasic phosphate of sodium	0·2
	Carbonate of sodium	0·28
	Sulphate of sodium	0·28
	Phosphates of calcium and magnesium	0·25
	Oxide and phosphate of iron	0·5
Odoriferous and colouring matter, gases, creatin, urea, and other extractive matters, glucose, and accidental substances		6·40
		1000·

Elementary composition of the dried blood of the ox:—

Carbon	57·9
Hydrogen	7·1
Nitrogen	17·4
Oxygen	19·2
Ashes	4·4

These results of the ultimate analysis of ox's blood afford a remarkable illustration of its general purpose, as supplying the materials for the

renovation of all the tissues. For the analysts (Playfair and Boeckmann) have found that the flesh of the ox yields the same elements in so nearly the same proportions, that the elementary composition of the organic constituents of the blood and flesh may be considered identical, and may be represented for both by the formula $C_{48}H_{39}N_6O_{15}$.

The Blood-Corpuscles or Blood-Cells.

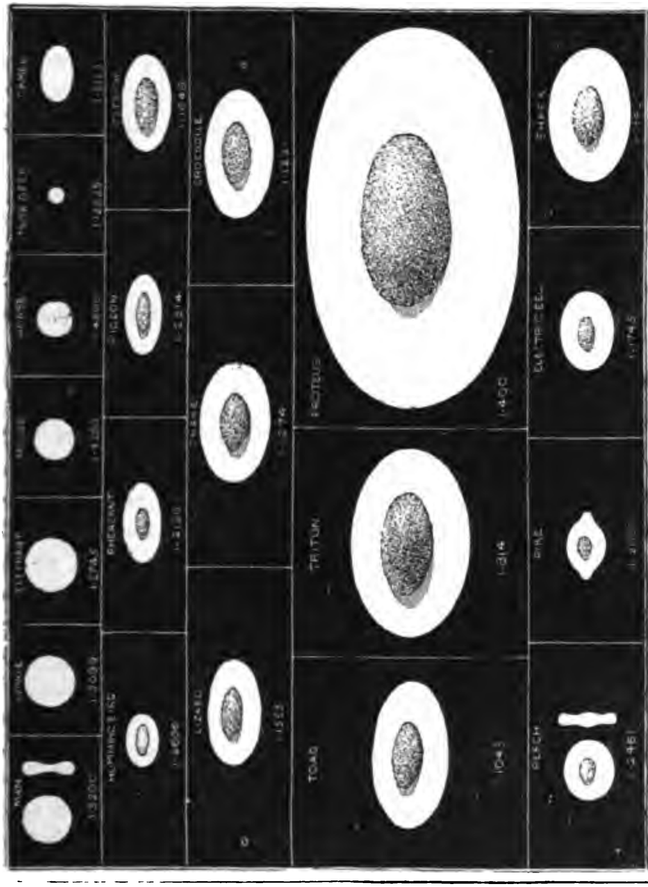
It has been already said, that the clot of blood contains, with the fibrin and the portion of the serum that is soaked in it, the *blood-corpuscles* or *blood-cells*. Of these there are two principal forms, the *red* and the *white* corpuscles, or, as they are now frequently named, the *coloured* and the *colourless*. When coagulation has taken place quickly, both kinds of corpuscles may be uniformly diffused through the clot; but when it has been slow, the red corpuscles, being the heaviest constituent of the blood, tend by gravitation to accumulate at the bottom of the clot; and the white corpuscles, being among the lightest constituents, collect in the upper part, and contribute to the formation of the buffy coat. In the moist state, the red corpuscles form 45 per cent. by weight, of the whole mass of the blood. (Robin.)

Physical and Chemical Characters of Red Blood-Corpuscles.

The *human red blood-cells or blood-corpuscles* (figs. 63 and 67) are circular or coin-shaped flattened disks, varying in diameter from $\frac{1}{3000}$ to $\frac{1}{4000}$ of an inch, and about $\frac{1}{10000}$ of an inch in thickness. In other words, if placed flat, edge to edge, about ten millions would lie on a square inch of surface. Their borders are rounded; their surfaces, in the perfect and most usual state, slightly concave; but they readily acquire flat or convex surfaces when, the liquor sanguinis being diluted, they are swollen by absorption of fluid. When viewed singly, they appear of a pale yellowish tinge; the deep red colour which they give to the blood being observable in them only when they are seen *en masse*. They are composed of a colourless, structureless, and transparent filmy framework or *stroma*, infiltrated in all parts by a red colouring-matter termed *hæmoglobin*. The *stroma* is tough and elastic, so that, as the cells circulate, they admit of elongation

Fig. 54.*

Mammals. Birds. Reptiles. Amphibia. Fish.



* The above illustration is somewhat altered from a drawing, by Mr. Gulliver, in the Proceed. Zool. Society, and exhibits the typical characters of the red blood-cells in the main divisions of the Vertebrata. The fractions are those of an inch, and represent the average diameter. In the case of the oval cells, only the long diameter is here given. It is remarkable, that although the size of the red blood-cells varies so much in the different classes of the vertebrate kingdom, that of the white corpuscles remains comparatively uniform, and thus they are, in some animals, much greater, in others much less than the red corpuscles existing side by side with them.

and other changes of form, in adaptation to the vessels, yet recover their natural shape as soon as they escape from compression. The term cell, in the sense of a bag or sac, is inapplicable to the red blood-corpuscle; and it must be considered, if not solid throughout, yet as having no such variety of consistence in different parts as to justify the notion of its being a membranous sac with fluid contents. The stroma exists in all parts of its substance, and the colouring-matter uniformly pervades this, and is not merely surrounded by and mechanically enclosed within the outer wall of the corpuscle. The red corpuscles have no nuclei, although, in their usual state, the unequal refraction of transmitted light gives the appearance of a central spot, brighter or darker than the border, according as it is viewed in or out of focus. Their specific gravity is about 1088.

In examining a number of red corpuscles with the microscope, it is easy to observe certain natural diversities among them, though they may have been all taken from the same part. The great majority, indeed, are very uniform; but some are rather larger, and the larger ones generally appear paler and less exactly circular than the rest; their surfaces also are, usually, flat or slighty convex, they often contain a minute shining particle like a nucleolus, and they are lighter than the rest, floating higher in the fluid in which they are placed. Other deviations from the general characters assigned to the corpuscles, depend on changes that occur after they are taken from the body. Very commonly they assume a granulated or mulberry-like form, in consequence, apparently, of a peculiar corrugation of their cell-walls. Sometimes, from the same cause, they present a very irregular, jagged, indented, or star-like appearance. The larger cells are much less liable to this change than the smaller, and the natural shape may be restored by diluting the fluid in which the corpuscles float.

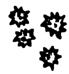
Action of Reagents.—Considerable light has been thrown on the physical and chemical constitution of red blood cells by studying the effects produced by various reagents: the following is a brief summary of these reactions:—

Pressure.—If the red blood-cells of a frog or man are gently squeezed, they exhibit a wrinkling of the surface, which clearly indicates that there is

a superficial pellicle partly differentiated from the softer mass within; again, if a needle be rapidly drawn across a drop of blood several corpuscles will be found cut in two; but this is not accompanied by any escape of cell-contents; the two halves, on the contrary, assume a rounded form, proving clearly that the corpuscles are not mere membranous sacs with fluid contents like fat-cells.

Fluids—Water.—When water is added gradually to frog's blood, the oval disc-shaped corpuscles become spherical, and gradually discharge their hæmoglobin, a pale, transparent stroma being left behind; human red blood-cells change from a discoidal to a spheroidal form, and discharge their cell-contents, becoming quite transparent and all but invisible.

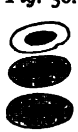
Fig. 55.



Solution of common salt (dilute) produces no appreciable effect on the red blood-cells of the frog. In the red blood-cells of man the discoid shape is exchanged for a spherical one, with spinous projections, like a horse-chestnut. Their original forms can be at once restored by the use of carbonic acid.

Acetic acid (dilute) causes the nucleus of the red blood-cells in the frog to become more clearly defined; if the action is prolonged, the nucleus becomes strongly granulated, and all the colouring matter seems to be concentrated in it, the surrounding cell-substance and outline of the cell becoming almost invisible; after a time the cells lose their colour altogether. The cells in the figure represent the successive stages of the change. A similar loss of colour occurs in the red cells of human blood.

Fig. 56.

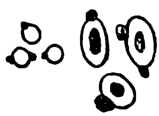


Alkalies cause the red blood-cells to swell and finally disappear.

Chloroform added to the red blood-cells of the frog causes them to part with their hæmoglobin; the stroma of the cells becomes gradually broken up, the nucleus resisting disintegration longest. A similar effect is produced on the human red blood-cell.

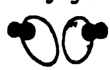
Tannin.—When a 2 per cent. solution of tannic acid is applied to frogs' blood it causes the appearance of a sharply-defined little knob, projecting from the free surface: the colouring matter becomes at the same time concentrated in the nucleus, which grows more distinct. A similar effect is produced on the human red blood-cell. (Roberts.) *Magenta*, when applied to the red blood-cells of the frog, produces a similar little knob or knobs, at the same time staining the nucleus and causing the discharge of the hæmoglobin. (Roberts.) The first effect of the magenta is to cause the discharge of the hæmoglobin, then the nucleus becomes suddenly stained, and lastly a finely granular matter issues through the wall of the corpuscle, becoming stained by the magenta, and a macula is formed at the point of escape. A similar *macula* is produced in the human red blood-cell.

Fig. 57.



Boracic Acid.—A 2 per cent. solution applied to nucleated red blood-cells (frog) will cause the concentration of all the colouring matter in the nucleus; the coloured body thus formed gradually quits its central position and comes to be partly, sometimes entirely, protruded from the surface of the now colourless cell. The result of this experiment led Brücke to distinguish the

Fig. 58.



coloured contents of the cell (zooid) from its colourless stroma (œcoid). When applied to the non-nucleated mammalian corpuscle, its effect merely resembles that of other dilute acids.

Gases—Carbonic Acid.—If the red blood-cells of a frog be first exposed to the action of water-vapour (which renders their outer pellicle more readily permeable to gases), and then acted on by carbonic acid, the nuclei immediately become clearly defined and strongly granulated; when air or oxygen is admitted the original appearance is at once restored. The upper and lower cell in the figure show the effect of carbonic acid; the middle one the effect of the re-admission of air. These effects can be reproduced five or six times in succession. If, however, the action of the carbonic acid be much prolonged, the granulation of the nucleus becomes permanent; it appears to depend upon a coagulation of the paraglobulin. (Stricker.)

Fig. 59.

Fig. 60.

Ammonia.—Its effects seem to vary according to the degree of concentration. Sometimes the outline of the corpuscles becomes distinctly crenated; at other times the effect resembles that of boracic acid, while in other cases the edges of the corpuscles begin to break up. (Lankester.)

Heat.—The effect of heat up to 50—60° C. is to cause the formation of a number of bud-like processes.

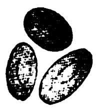
Fig. 61.

Electricity causes the red blood-corpuscles to become crenated, and at length mulberry-like. Finally they recover their round form and become quite pale.

The general conclusions to be drawn from these observations have been summed up as follows by Mr. Ray Lankester:—

"The red blood-corpuscle of the vertebrata is a viscid, and at the same time elastic disc, oval, or round, in outline, its surface being differentiated somewhat from the underlying material, and forming a pellicle or membrane of great tenuity, not distinguishable with the highest powers (whilst the corpuscle is normal and living), and having no pronounced inner limitation. The viscid mass consists of (or rather *yields*, since the state of combination of the components is not known) a variety of albuminoid and other bodies, the most easily separable of which is hæmoglobin; secondly, the matter which segregates to form Roberts's macula; and thirdly, a residuary stroma, apparently homogeneous in the mammalia (excepting as far as the outer surface or pellicle may be of a different chemical nature), but containing in the other vertebrata a sharply definable nucleus, this nucleus being already differentiated, but not sharply delineated during life, and consisting of (or separable into) at least two components, one (paraglobulin) precipitable by CO_2, and removable by the action of weak NH_3; the other pellucid, and not granulated by acids."

Fig. 62.



A peculiar property of the red corpuscles, which is exaggerated in inflammatory blood, may be here noticed. It gives them a great tendency to adhere together in rolls or columns, like piles of coins, and then, very quickly, these rolls fasten together by

their ends, and cluster; so that, when the blood is spread out thinly on a glass, they form a kind of irregular network, with crowds of corpuscles at the several points corresponding with the knots of the net (fig. 63). Hence, the clot formed in such a thin layer of blood looks mottled with blotches of pink upon a white ground: in a larger quantity of such blood, as soon as the corpuscles have clustered and collected in rolls (that is, generally in two or three minutes after the blood is drawn), they begin to sink very quickly; for in the aggregate they present less surface to the resistance of the liquor sanguinis than they would if sinking separately. Thus quickly sinking, they leave above them a layer of liquor sanguinis, and this coagulating, forms a buffy coat, as before described, the volume of which is augmented by the white corpuscles, which have no tendency to adhere to the red ones, and by their lightness float up clear of them.

Fig. 63.*

This tendency, on the part of the red corpuscles, to form rouleaux, is probably, as Dr. Norris suggests, only a physical phenomenon, comparable to the collection into somewhat similar rouleaux of discs of cork when they are partially immersed in water.

Chemical Characters.—As they exist in the blood, the coloured corpuscles contain three-fourths of their weight of water.

The *stroma* is composed of globulin, protagon, fatty matters, including cholesterin, and salts, chiefly phosphates of potassium, sodium, and calcium. The stroma is infiltrated, as before mentioned (p. 110), with a red colouring matter termed *hæmoglobin*.

Hæmoglobin, which enters far more largely into the composition of the coloured corpuscles than any other ingredient, is an albuminous compound with the following composition:—

* Fig. 63. Red corpuscles in rouleaux. At *a*, *a*, are two white corpuscles.

Carbon	54·0
Hydrogen	7·25
Nitrogen	16·25
Oxygen	21·45
Sulphur	0·63
Iron	0·42
	100·00

Allied as it is in chemical composition to albumin, hæmoglobin differs remarkably from it in many of its properties. The most interesting and important of these, physiologically considered, are (*a*) its power of crystallizing, the so-called *blood-crystals* being the natural crystalline forms of hæmoglobin; and (*b*) its attraction for oxygen and some other gases.

Hæmoglobin can be obtained in a crystalline form with various degrees of difficulty from the blood of different animals, that of man holding an intermediate place in this respect. Among the animals whose blood colouring-matter crystallizes most readily are the guinea-pig and the dog; and in these cases to obtain crystals it is generally sufficient to dilute a drop of recently drawn blood with water and expose it for a few minutes to the air.

Light seems to favour the formation of crystals. In many instances, however, other means must be adopted, *e.g.*, the addition of alcohol, ether, or chloroform, rapid freezing and then thawing, an electric current, a temperature of 60° C., or the addition of sodium sulphate. Hæmoglobin, though soluble in water, and, as we have seen, crystallisable, is not diffusible, *i.e.*, its solution cannot pass through the pores of an animal membrane. When heated, its solution coagulates, the hæmoglobin being decomposed into an albuminous substance, *globulin*, and a colouring matter, *hæmatin*.

A similar separation can be effected by the action of some acids and alkalies. Hæmatin was once thought to be the natural colouring matter of the blood, but is now known to be a product of the decomposition of hæmoglobin.

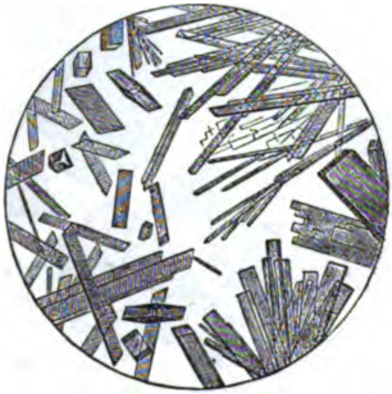
Another very important derivative of hæmoglobin is *Hæmin* or *Hydrochlorate of Hæmatin*, which may be prepared as follows:—

A small portion of a dried drop of blood is placed on a glass slide, together with a few small crystals of common salt. A thin glass cover is put on, and a drop of glacial acetic acid introduced beneath it: heat is gradually applied, and the excess of salt washed away with water. A number of small brownish crystals of a rhombic shape are thus formed. The formation of these hæmin crystals is of great interest and importance in a medico-legal point of view, as it constitutes the most certain and delicate test we have for the presence of blood in a stain on clothes, &c. It exceeds in delicacy even the spectroscopic test to be mentioned further on.

Different forms of blood-crystals are shown in the accompanying figures (Figs. 64, 65 and 66).

Another most important character of hæmoglobin is its attraction for oxygen, with which it enters into definite chemical combination (oxyhæmoglobin).

*Fig. 64.**



Oxyhæmoglobin readily parts with its combined oxygen in the presence of reducing agents, or even in vacuo; and on this, not less than on its readiness to combine with oxygen, depends its most important physiological properties.

During the passage of the blood through the lungs, the compound with oxygen is constantly formed; while it is as constantly decomposed, in consequence of the readiness with which hæmoglobin parts with oxygen, when the latter is exposed to other attractions in its circulation through the systemic capillaries. Thus, the red corpuscles, in virtue of their colouring matter, which readily absorbs oxygen and as readily gives it up again, are the chief means by which this gas is carried in the blood; and to the chemical changes thus produced in hæmoglobin is to be attributed the chief

Fig. 65.†

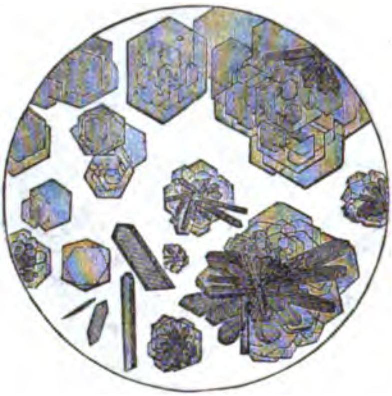
Figs. 64, 65, 66, illustrate some of the principal forms of blood-crystals:—

* Fig. 64. Prismatic, from human blood.

† Fig. 65. Tetrahedral, from blood of the guinea-pig.

share in the alteration of the colour of the blood in its passage from the arteries to the veins and *vice versâ* (see p. 124).

Fig. 66.*



Nitrous oxide forms a combination with hæmoglobin, which gives two absorption bands, very similar to those of oxyhæmoglobin (p. 124). Carbonic oxide possesses the property of entirely replacing the oxygen in oxyhæmoglobin, and its combination with hæmoglobin has a spectrum very closely resembling that of oxyhæmoglobin.

Distribution of Hæmoglobin.—In connection with the ascertained function of hæmoglobin as the great oxygen-carrier, the following facts with regard to its distribution are of importance. It occurs not only in the red blood-cells of all vertebrata except one fish (leptocephalus) whose blood-cells are all colourless, but also in similar cells in many worms: moreover it is found diffused in the vascular fluid of some other worms and certain crustacea; it also occurs in all the striated muscles of mammals and birds. It is generally absent from unstriated muscle except that of the rectum. It has also been found in mollusca in certain muscles which are specially active, viz., those which work the rasp-like tongue.

In the muscles of fish it has hitherto only been met with in the very active muscle which moves the dorsal fin of the Hippocampus (Ray Lankester)

The White Corpuscles of the Blood or Blood-Leucocytes.

The *white* or colourless corpuscles of the blood, which are identical with lymph-corpuscles, are much less numerous than the *red*. On an average, in health, there may be one white to 400 or 500 red corpuscles; but in disease, the proportion is often as high as one to ten, and sometimes even much higher.

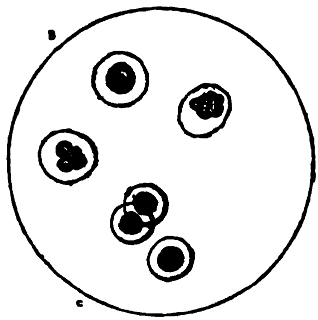
In health, the proportion varies considerably even in the course of the same day. The variations appear to depend chiefly

* Fig. 66. Hexagonal crystals, from blood of squirrel. On these six-sided plates, prismatic crystals, grouped in a stellate manner, not unfrequently occur (after Funke).

on the amount and probably also on the kind of food taken; the number of leucocytes being very considerably increased by a meal, and diminished again on fasting. Also in young persons, during pregnancy, and after great loss of blood, there is a larger proportion of colourless blood-corpuscles, which probably shows that they are more rapidly formed under these circumstances. In old age, on the other hand, their proportion is diminished.

They present greater diversities of form than the red ones do; but the gradations between the extreme forms are so regular, that no sufficient reason can be found for supposing that there is in healthy blood more than one species of white corpuscles. In their most general appearance, they are globular, and are about $\frac{1}{2500}$ of an inch in diameter (*a*, fig. 63). They have a greyish, pearly look, appearing variously shaded or nebulous, the shading being much darker in some than in others. They consist of protoplasm containing granules which are in some specimens few and very distinct, in others (though rarely) so numerous that the whole corpuscle looks like a mass of granules.

Fig. 67.*



These corpuscles cannot be said to have any true cell-wall. In a few instances an apparent cell-membrane can be traced around them; but, much more commonly, even this is not discernible till after the addition of water or dilute acetic acid (Fig. 67).

A remarkable property of the colourless corpuscles, first observed by Mr. Wharton Jones, consists in their capability of spontaneously changing their shape. If a drop of blood be examined with a high microscope-power under conditions by which loss of moisture is prevented, at the same time that the

* Fig. 67. Red and white blood-corpuscles. *b*, Three white corpuscles acted on by weak acetic acid. *c*, Red blood-corpuscles.

temperature is maintained at about the degree natural to the blood as it circulates in living body, the leucocytes can be seen alternately contracting and dilating very slowly at various parts of their circumference,—shooting out irregular processes, and again withdrawing them partially or completely, and thus in succession assuming various irregular forms (p. 46).

Fig. 68.*

These *amœboid* movements (p. 46) are characteristic of the living leucocyte, and form a good example of the contractile property of protoplasm, before referred to. Indeed, the unchanging rounded form which the corpuscles present in ordinary microscopic specimens must be looked upon as the shape natural to a dead corpuscle, or one whose vitality is dormant, rather than as the proper shape of one living and active.

In many lower vertebrata, such as the newt, two or three distinct kinds of colourless blood corpuscles may be distinguished, and their movements are both more rapid, and the resulting changes of form more extreme, than in human colourless corpuscles.

Action of Reagents.—*Water* checks the amœboid movements and causes the corpuscle to become globular: the nuclei, when multiple, coalesce into one, and the cell suddenly bursts, discharging its contents.

Acetic Acid (dilute) causes the cessation of the amœboid movements and the clear definition of the nucleus or nuclei, together with the appearance of granules. (Fig. 67.)

If some fine pigment-granules be added to a fluid containing colourless blood-corpuscles, on a glass slide, these will be observed, under the microscope, to take up the pigment. In some cases colourless blood-corpuscles have been seen with fragments of coloured ones thus imbedded in their substance.

Colourless blood-corpuscles have been observed to multiply by fission.

The *locomotion* of leucocytes has been already referred to (p. 71).

* Fig. 68. Human colourless blood-corpuscle, showing its successive changes of outline within ten minutes when kept moist on a warm stage (Schofield).

Besides the red and white corpuscles, the microscope reveals numerous minute *molecules* or *granules* in the blood, circular or spherical, and varying in size from the most minute visible speck to the $\frac{1}{8000}$ of an inch (Gulliver). These molecules are very similar to those found in the lymph and chyle, and are some of them, fatty (being soluble in ether), others probably albuminous. Generally, also, there may be detected in the blood, especially during the time of active digestion, very minute equal-sized fatty particles, similar to those of which the molecular base of chyle is constituted (Gulliver).

The Serum.

The *serum* is the liquid part of the blood remaining after the coagulation of the fibrin. In the usual mode of coagulation, part of the serum remains in the clot, and the rest, squeezed from the clot by its contraction, lies around it. The quantity of serum that appears around the clot depends partly on the total quantity in the blood, but partly also on the degree to which the clot contracts. This is affected by many circumstances: generally, the faster the coagulation the less is the amount of contraction; and, therefore, when blood coagulates quickly, it will appear to contain a small proportion of serum. In all cases, too, it should be remembered, that, since the contraction of the clot may continue for thirty-six or more hours, the quantity of serum in the blood cannot be even roughly estimated till this period has elapsed.

The serum is an alkaline, yellowish fluid, with a specific gravity of from 1025 to 1030. It is composed mainly of water, in which are dissolved all the substances enumerated in the table (p. 109), excepting the fibrin and corpuscles.

The *water of the blood* is subject to hourly variations in its quantity, according to the period since the taking of food, the amount of bodily exercise, the state of the atmosphere, and all the other events that may affect either the ingestion or the excretion of fluids. According to these conditions, it may vary from 700 to 790 parts in the thousand. Yet uniformity is on the whole maintained; because nearly all those things which tend to lower the proportion of water in the blood, such as active exercise, or the addition of saline or other solid matter, excite thirst; while, on the other hand, the addition of an excess of water to the blood is quickly followed by its more

copious excretion in sweat and urine. And these means for adjusting the proportion of the water find their purpose in maintaining certain important physical conditions in the blood; such as its proper viscidity, and the degree of its adhesion to the vessels through which it ought to flow with the least possible resistance from friction. On this also depends, in great measure, the activity of absorption by the blood-vessels, into which no fluids will quickly penetrate, but such as are of less density than the blood. Again, the quantity of water in the blood determines chiefly its volume, and thereby the fulness and tension of the vessels and the quantity of fluid that will exude from them to keep the tissues moist. Finally, the water is the general solvent of all the other materials of the liquor sanguinis.

It is remarkable, that the proportion of water in the blood may be sometimes increased even during its abstraction from an artery or vein. Thus Dr. Zimmermann in bleeding dogs, found the last drawn portion of blood contain 12 or 13 parts more of water in 1000 than the blood first drawn; and Polli noticed a corresponding diminution in the specific gravity of the human blood during venesection, and suggested the only probable explanation of the fact, namely, that during bleeding, the blood-vessels absorb very quickly a part of the serous fluid with which all the tissues are moistened.

The *albumen* may vary, consistently with health, from 60 to 70 parts in the 1000 of blood. It is, probably, in combination with soda, as an albuminate of soda; for, if serum be much diluted with water, and then neutralized with acetic acid, pure albumen is deposited. Another view entertained by Enderlin is that the albumen is dissolved in the solution of the neutral phosphate of sodium, to which he considers the alkaline reaction of the blood to be due, and solutions of which can dissolve large quantities of albumen and phosphate of calcium.

The proportion of *fibrin* in healthy blood may vary between 2 and 3 parts in 1000. In some diseases, such as typhus, and others of low type, it may be as little as 1·034; in other diseases, it is said, it may be increased to as much as 7·528 parts in 1000. But in all these analyses it must be remembered that the white corpuscles are also included, inasmuch as it is impossible to separate them from the fibrin.

The *fatty* matters are subject to much variation in quantity, being commonly increased after every meal in which fat has been taken. At such times, the fatty particles of the chyle, added quickly to the blood, are only gradually assimilated; and their quantity may be sufficient to make the serum of the blood opaque, or even milk-like.

Variations in healthy Blood under different Circumstances.

The conditions which appear most to influence the composition of the blood in health, are these: sex, pregnancy, age, and temperament. The composition of the blood is also, of course, much influenced by diet.

1. *Sex.*—The blood of men differs from that of women, chiefly in being of somewhat higher specific gravity, from its containing a relatively larger quantity of red corpuscles.

2. *Pregnancy.*—The blood of pregnant women has a rather lower specific gravity than the average, from deficiency of red corpuscles. The quantity of white corpuscles, on the other hand, and of fibrin, is increased.

3. *Age.*—From the analysis of Denis it appears that the blood of the fœtus is very rich in solid matter, and especially in red corpuscles; and this condition, gradually diminishing, continues for some weeks after birth. The quantity of solid matter then falls during childhood below the average, again rises during adult life, and in old age falls again.

4. *Temperament.*—But little more is known concerning the connection of this with the condition of the blood, than that there appears to be a relatively larger quantity of solid matter, and particularly of red corpuscles, in those of a plethoric or sanguineous temperament.

5. *Diet.*—Such differences in the composition of the blood as are due to the temporary presence of various matters absorbed with the food and drink, as well as the more lasting changes which must result from generous or poor diet respectively, need be here only referred to.

Effects of Bleeding.—The result of bleeding is to diminish the specific gravity of the blood; and so quickly, that in a single venesection, the portion of blood last drawn has often a less specific gravity than that of the blood that flowed first (J. Davy and Polli). This is, of course, due to absorption of fluid from the tissues of the body. The physiological import of this fact, namely, the instant absorption of liquid from the tissues, is the same as that of the intense thirst which is so common after either loss of blood, or the abstraction from it of watery fluid, as in cholera, diabetes, and the like.

For some little time after bleeding, the want of red blood-cells is well marked; but with this exception, no considerable alteration seems to be produced in the composition of the blood for more than a very short time; the loss of the other constituents, including the pale corpuscles, being very quickly repaired.

Variations in the Composition of the Blood, in different Parts of the Body.

The composition of the blood, as might be expected, is found to vary in different parts of the body. Thus arterial blood differs from venous; and although its composition and general characters are uniform throughout the whole course of the systemic arteries, they are not so throughout the venous system, —the blood contained in some veins differing remarkably from that in others.

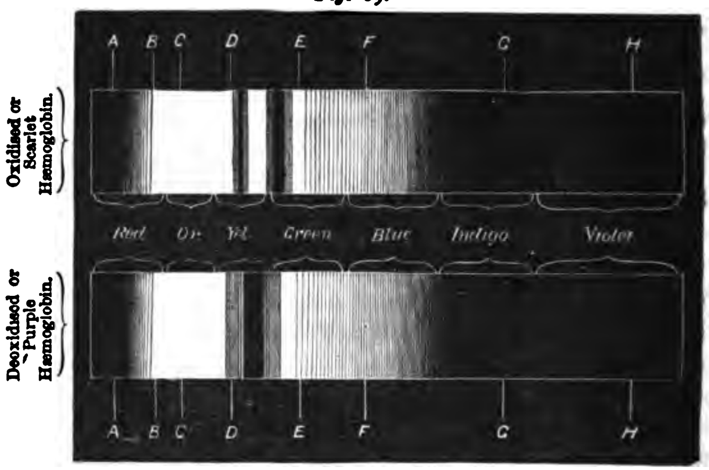
1. *Differences between arterial and venous blood.*—These may be arranged under two heads,—differences in *colour*, and in *general composition.*

The colouring matter of the blood, or hæmoglobin (p. 115), is capable of existing in two different states of oxidation, and the respective colours of

arterial and venous blood are caused by differences in tint between these two varieties—*scarlet hæmoglobin* or *oxy-hæmoglobin* and *deoxidised* or *purple* hæmoglobin. The change of colour produced by the passage of the blood through the lungs, and its consequent exposure to oxygen, is due, chiefly, to the oxidation of purple, and its conversion into scarlet hæmoglobin; while the readiness with which the latter is de-oxidised offers a reasonable explanation of the change, in regard to tint, of arterial into venous blood,—the transformation being effected by the delivering up of oxygen to oxidisable matters, by the scarlet hæmoglobin, during the blood's passage through the capillaries. Formerly carbonic acid was believed to make blood dark by causing the red corpuscles to assume a bi-convex shape, while oxygen was thought to reverse the effect by contracting them and rendering them bi-concave. But although we are not in a position to deny altogether the possible influence of mechanical conditions of the red corpuscles on the colour of arterial and venous blood respectively, it is probable that this cause alone would be quite insufficient to explain the differences in the colour of the two kinds of blood, and therefore if it be an element at all in the change, it must be allowed to take only a subordinate position.

The distinction between the two kinds of hæmoglobin naturally present in the blood, or in other words, the proof that the addition or subtraction of oxygen involves the production of two substances having fundamental differences of chemical constitution, has been made out chiefly by *spectrum-*

Fig. 69.*



*analysis.** For while a solution of oxy-hæmoglobin, causes the appearance of two absorption bands in the yellow and the green part of the *spectrum*, between D and E, these are replaced by a single band intermediate in position,

* The student to whom the terms employed in connection with spectrum-analysis are not familiar, is advised to consult, with reference to this paragraph, an elementary treatise on Physics.

when the oxidised or scarlet solution is darkened by de-oxidising agencies,—or, in other words, when the change which naturally ensues in the conversion of arterial into venous blood is artificially produced. (Stokes.)

The greater part of the hæmoglobin in both arterial and venous blood exists in the scarlet or more highly oxidised condition, and only a small part is de-oxidised and made purple in its passage from the arteries into the veins.

The differences in regard to colour between arterial and venous blood are sometimes not to be observed. If blood runs very slowly from an artery, as from the bottom of a deep and devious wound, it is often as dark as venous blood. In persons nearly asphyxiated also, and sometimes, under the influence of chloroform or ether, the arterial blood becomes like the venous. In the fœtus also both kinds of blood are dark. But, in all these cases, the dark blood becomes bright on exposure to the air. Bernard has shown that venous blood returning from a gland in active secretion is almost as bright as arterial blood.

b. General Composition.—The chief differences between arterial and ordinary venous blood are these. Arterial blood contains rather more fibrin, and rather less albumen and fat. It coagulates somewhat more quickly. Also, it contains more oxygen, and less carbonic acid. According to Denis, the fibrin of venous blood differs from arterial, in that when it is fresh and has not been much exposed to the air, it may be dissolved in a slightly heated solution of nitrate of potassium.

Some of the veins contain blood which differs from the ordinary standard considerably. These are the portal, the hepatic, and the splenic veins.

Portal vein.—The blood which the portal vein conveys to the liver is supplied from two chief sources; namely, that in the gastric and mesenteric veins, which contains the soluble elements of food absorbed from the stomach and intestines during digestion, and that in the splenic vein; it must, therefore, combine the qualities of the blood from each of these sources.

The blood in the gastric and mesenteric veins will vary much according to the stage of digestion and the nature of the food taken, and can therefore be seldom exactly the same. Speaking generally, and without considering the sugar, dextrin, and other soluble matters which may have been absorbed from the alimentary canal, this blood appears to be deficient in solid matters, especially in red corpuscles, owing to dilution by the quantity of water absorbed, to contain an excess of albumen, and to yield a less tenacious kind of fibrin than that of blood generally.

The blood from the splenic vein is generally deficient in red corpuscles, and contains an unusually large proportion of albumen. The fibrin seems to vary in relative amount, but to be almost always above the average. The proportion of colourless corpuscles is also unusually large. The whole quantity of solid matter is decreased, the diminution appearing to be chiefly in the proportion of red corpuscles.

The blood of the portal vein, combining the peculiarities of its two factors, the splenic and mesenteric venous blood, is usually of lower specific gravity than blood generally, is more watery, contains fewer red corpuscles, more

albumen, chiefly in the form of albuminose, and yields a less firm clot than that yielded by other blood, owing to the deficient tenacity of its fibrin. These characteristics of portal blood refer to the composition of the blood itself, and have no reference to the extraneous substances, such as the absorbed materials of the food, which it may contain; neither, indeed, has any complete analysis of these been given.

Comparative analyses of blood in the portal vein and blood in the hepatic veins have also been frequently made, with the view of determining the changes which this fluid undergoes in its transit through the liver. Great diversity, however, is observable in the analyses of these two kinds of blood by different chemists. Part of this diversity is no doubt attributable to the fact pointed out by Bernard, that unless the portal vein is tied before the liver is removed from the body, hepatic venous blood is very liable to regurgitate into the portal vein, and thus vitiate the result of the analysis. Guarding against this source of error, recent observers have determined that hepatic venous blood contains less water, albumen, and salts, than the blood of the portal vein; but that it yields a much larger amount of extractive matter, in which, according to Bernard and others, is one constant element, namely, grape-sugar, which is found, whether saccharine or farinaceous matter have been present in the food or not.

Besides the rather wide difference between the composition of the blood of these veins and of others, it must not be forgotten that in its passage through every organ and tissue of the body, the blood's composition must be varying constantly, as each part takes from it or adds to it such matter as it, roughly speaking, wishes either to have or to throw away. Thus the blood of the renal vein has been proved by experiment to contain less water than does the blood of the artery, and doubtless its salts are diminished also. The blood in the renal vein is said, moreover, by Bernard and Brown-Séquard not to coagulate.

This then is an example of the change produced in the blood by its passage through a special excretory organ. But all parts of the body,—bones, muscles, nerves, etc.,—must act on the blood as it passes through them, and leave in it some mark of their action, too slight though it may be, at any given moment, for analysis by means now at our disposal.

The Gases of the Blood.

The gases contained in the blood are carbonic acid, oxygen, and nitrogen, 100 volumes of blood containing from 40 to 50 volumes of these gases collectively.

Arterial blood contains relatively more oxygen and less carbonic acid than venous. But the absolute quantity of carbonic acid is in both kinds of blood greater than that of the oxygen.

	Oxygen.	*Carbonic Acid.*
Arterial Blood	16·9 vol. per cent.	30 vol. per cent.
Venous " (from muscles at rest) .	5·96 " " "	35 " " "

The proportion of nitrogen is in both very small, (1—2 vols. per cent.).

The carbonic acid of the blood is partly in a state of simple solution, and partly in a state of weak chemical combination. That portion of the carbonic acid which is chemically combined, is contained partly in bicarbonate of sodium, and partly is united with phosphate of the same base.

The oxygen is, almost all of it, combined chemically with the hæmoglobin of the red corpuscles (pp. 117 and 124).

That the oxygen is absorbed chiefly by the red corpuscles is proved by the fact that while blood is capable of absorbing oxygen in considerable quantity, the serum alone has little or no more power of absorbing this gas than pure water.

Development of the Blood.

In the development of the blood little more can be traced than the processes by which the corpuscles are formed.

The first formed blood-cells of the human embryo differ much in their general characters from those which belong to the latter periods of intra-uterine, and to all periods of extra-uterine life. Their manner of origin differs also, and it will be well perhaps to consider this first.

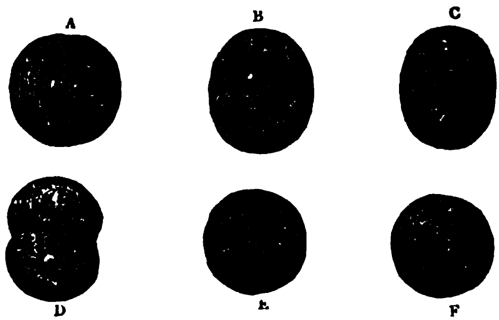
The formation of the first blood corpuscles is very simple. While the outermost of the embryonic cells, of which the rudimentary heart and its attendant vessels are composed, gradually develop into the muscular and other tissues which form the walls of the heart and blood-vessels, the inner cells simply separate from each other, and form blood-cells; some fluid plasma being at the same time secreted. Thus, by the same process, blood is formed, and the originally solid heart and blood-vessels are hollowed out.

The blood-cells produced in this way, are from about $\frac{1}{2500}$ to $\frac{1}{1500}$ of an inch in diameter, mostly spherical, pellucid, and colourless, with granular contents, and a well-marked nucleus. Gradually, they acquire a red colour, at the same time that the nucleus becomes more defined, and the granular matter clears

away. Sir J. Paget describes them as, at this period, circular, thickly disc-shaped, full-coloured, and, on an average, about $\frac{1}{2500}$ of an inch in diameter; their nuclei, which are about $\frac{1}{5000}$ of an inch in diameter, are central, circular, very little prominent on the surfaces of the cell, and apparently slightly granular or tuberculated.

Before the occurrence, however, of this change—from the colourless to the coloured state—in many instances, probably, during it, and in many afterwards, a process of multiplication takes place by division of the nucleus and subsequently of the cell, into two, and much more rarely, three or four new cells, which gradually acquire the characters of the original cell from which they sprang. (Fig. 70.)

Fig. 70.*



When, in the progress of embryonic development, the liver begins to be formed, the multiplication of blood-cells in the whole mass of blood ceases, according to Kölliker, and new blood-cells are produced by this organ. Like those just described, they are at first colourless and nucleated, but afterwards acquire the ordinary blood-tinge, and resemble very much those

* Fig. 70. Development of the first set of blood-corpuscles in the mammalian embryo. A. A dotted, nucleated embryo-cell in process of conversion into a blood-corpuscle: the nucleus provided with a nucleolus. B. A similar cell with a dividing nucleus; at C, the division of the nucleus is complete; at D, the cell also is dividing. E. A blood-corpuscle almost complete, but still containing a few granules. F. Perfect blood-corpuscle.

of the first set. Like them they may also multiply by division. In whichever way produced, however, whether from the original formative cells of the embryo, or by the liver, these coloured nucleated cells begin very early in fœtal life to be mingled with coloured non-nucleated corpuscles resembling those of the adult, and about the fourth or fifth month of embryonic existence are completely replaced by them.

The manner of origin of these perfect non-nucleated corpuscles must be now considered.

I. *Concerning the Cells from which they arise.*

a. Before Birth.—It is uncertain whether they are derived only from the cells of the lymph, which, at about the period of their appearance, begins to be poured into the blood; or whether they are derived also from the nucleated red cells, which they replace, or also from similar nucleated cells, which Kölliker thinks are produced by the liver during the whole time of fœtal existence.

b After Birth.—It is generally agreed that after birth the red corpuscles are derived from the smaller of the nucleated lymph or chyle-corpuscles,—*the white corpuscles of the blood.*

These white corpuscles are probably derived chiefly from the lymphatic glands, spleen, and the medulla of bone; they also originate from the cells shed off from the germinating portions of serous membranes, and taken up into the lymphatics through the stomata (p. 62).

II. *Concerning the Manner of their Development.*

There is not perfect agreement among physiologists concerning the process by which lymph-globules or white corpuscles (and in the fœtus, perhaps the red nucleated cells) are transformed into red non-nucleated blood-cells. For while some maintain that the whole cell is changed into a red one by the gradual clearing up of the contents, including the nucleus, it is believed by Mr. Wharton Jones and many others, that only the nucleus becomes the red blood-cell, by escaping from its envelope and acquiring the ordinary blood-tint.

Of these two theories the former is now the most generally accepted.

The following are the chief arguments in its favour:

The similarity of the action of reagents, especially tannin and magenta, on the non-nucleated red corpuscles of man, and the nucleated ones of the frog, would appear to show that they are fundamentally similar; and, in the frog, the transformation of the colourless into coloured corpuscles has been observed to take place. If frog's blood be collected and prevented from evaporating while the air around it is constantly renewed, this transformation of many colourless corpuscles occurs in the course of two or three weeks. The colour can be observed spreading from the centre of the cells towards their periphery (Recklinghausen).

The development of red blood-cells from the corpuscles of the lymph and chyle continues throughout life, and there is no reason for supposing that after birth they have any other origin.

Without doubt, these little bodies have, like all other parts of the organism, a tolerably definite term of existence, and in a like manner die and waste away when the portion of work allotted to them has been performed. Neither the length of their life, however, nor the fashion of their decay, has been yet clearly made out, and we can only surmise that in these things they resemble more or less closely those parts of the body which lie more plainly within our observation.

From what has been said, it will have appeared that when the blood is once formed, its *growth* and *maintenance* are effected by the constant repetition of the development of new portions. In the same proportion that the blood yields its materials for the maintenance and repair of the several solid tissues, and for secretions, so are new materials supplied to it in the lymph and chyle, and by development made like it. The part of the process which relates to the formation of new corpuscles has been described, but it is probably only a small portion of the whole process; for the assimilation of the new materials to the blood must be perfect, in regard to all those immeasurable minute particulars by which the blood is adapted for the nutrition of every

tissue, and the maintenance of every peculiarity of each. How precise the assimilation must be for such an adaptation, may be conceived from some of the cases in which the blood is altered by disease, and by assimilation is maintained in its altered state. For example, by the insertion of vaccine matter, the blood is for a short time manifestly diseased; however minute the portion of virus, it affects and alters, in some way, the whole of the blood. And the alteration thus produced, inconceivably slight as it must be, is long maintained; for even very long after a successful vaccination, a second insertion of the virus may have no effect, the blood being no longer amenable to its influence, because the new blood, formed after the vaccination, is made like the blood as altered by the vaccine virus; in other words, the blood exactly assimilates to its altered self the materials derived from the lymph and chyle. In health we cannot see the precision of the adjustment of the blood to the tissues; but we may imagine it from the small influences by which, as in vaccination, it is disturbed; and we may be sure that the new blood is as perfectly assimilated to the healthy standard as in disease it is assimilated to the most minutely altered standard.*

How far the assimilation of the blood is affected by any formative power which it may possess in common with the solid tissue, we know not. That this possible formative power is, however, if present, ministered to and assisted by the actions of other parts there can be no doubt; as *1st*, by the digestive and absorbent systems, and by the liver, and all of the so-called *vascular* glands; and, *2ndly*, by the excretory organs, which separate from the blood refuse materials, including in this term not only the waste substance of the tissues, but also such matters as, having been taken with food and drink, may have been absorbed from the digestive canal, and have been subsequently found unfit to remain in the circulating current. And, *3rdly*, the precise constitution of the blood is adjusted by the balance of the nutritive processes for maintaining the several tissues, so that none of the materials appropriate for the main-

* Corresponding facts in relation to the maintenance of the tissues by assimilation will be mentioned in the Chapter on NUTRITION.

tenance of any part may remain in excess in the blood. Each part, by taking from the blood the materials it requires for its maintenance, is, as has been observed, in the relation of an excretory organ to all the rest; inasmuch as by abstracting the matters proper for its nutrition, it prevents excess of such matter as effectually as if they were separated from the blood and cast out altogether by the excreting organs specially present for such a purpose.

Uses of the Blood.

1. To be a medium for the reception and storing of matter (ordinary food, drink, and oxygen) from the outer world, and for its conveyance to all parts of the body.

2. To be a source whence the various tissues of the body may take the materials necessary for their nutrition and maintenance; and whence the secreting organs may take the constituents of their various secretions.

3. To be a storehouse of *potential* energy, by the expenditure of which the heat of the body may be maintained, and, by correlation, vital and other force may be manifested.

4. To be a medium for the absorption of refuse matters, from all the tissues, and for their conveyance to those organs whose function it is to separate them and cast them out of the body.

5. To warm and moisten all parts of the body.

Uses of the various Constituents of the Blood.

Albumen.—Albumen, which exists in so large a proportion among the chief constituents of the blood, is without doubt mainly for the nourishment of those textures which contain it or other compounds nearly allied to it. Besides its purpose in nutrition, the albumen of the liquor sanguinis is doubtless of importance also in the maintenance of those essential physical properties of the blood to which reference has been already made.

Fibrin.—It has been mentioned in a previous part of this chapter that the idea of fibrin existing in the blood, as fibrin, is founded in error; and that it is formed in the act of coagulation by the union of two substances, which before existed separately (p. 105). In considering, therefore, the functions of fibrin, we may exclude the notion of its existence, as such, in the blood in a fluid state, and of its use in the nutrition of certain special textures, and look for the explanation of its functions to those circumstances, whether of health or disease, under which it is produced. In hæmorrhage, for example, the formation of fibrin in the clotting of blood, is the means by

which, at least for a time, the bleeding is restrained or stopped; and the material or *blastema* which is produced for the permanent healing of the injured part, contains a coagulable material identical, or very nearly so, with the fibrin of clotted blood.

Fatty Matters.—The fatty matters of the blood subserve more than one purpose. For while they are the means, in great part, by which the fat of the body, so widely distributed in the proper adipose and other textures, is replenished, they also, by their union with oxygen, assist in maintaining the temperature of the body. To certain secretions also, notably the milk and bile, fat is contributed.

Saline Matter.—The uses of the saline constituents of the blood are, first, to enter into the composition of such textures and secretions as naturally contain them, and, secondly, to assist in preserving the due specific gravity and alkalinity of the blood, and in preventing its decomposition. The phosphate and carbonate of sodium, to which the blood owes its alkaline reaction, preserve also the liquidity of its albumen, and favour its circulation through the capillaries, at the same time that they increase the absorptive power of the serum for gases. But although, from the constant presence of a certain quantity of saline matter in the blood, we may believe that it has these last-mentioned important functions in connection with the blood itself, apart from the nutrition of the body, yet, from the amount which is daily separated by the different excretory organs, and especially by the kidneys, we must also believe that a considerable quantity simply passes through the blood, both from the food and from the tissues, as a temporary and useless constituent, to be excreted when opportunity offers.

Corpuscles.—The uses of the red corpuscles are probably not yet fully known, but they may be inferred, in part, from the composition and properties of their contents. The affinity of hæmoglobin for oxygen has been already mentioned; and the main function of the red corpuscles seems to be the absorption of oxygen in the lungs by means of this constituent, and its conveyance to all parts of the body, especially to those tissues, the nervous and muscular, the discharge of whose functions depends in so great a degree upon a rapid and full supply of this element. The readiness with which hæmoglobin absorbs oxygen, and delivers it up again to a reducing agent, so well shown by the experiments of Prof. Stokes (p. 124), admirably adapts it for this purpose. How far the red corpuscles are concerned in the nutrition of the tissues is quite unknown.

The relation of the white to the red corpuscles of the blood has been already considered (p. 129); of the functions of the former, other than are concerned in this relationship, nothing is positively known. Recent observations of the migration of the white corpuscles from the interior of the blood-vessels into the surrounding tissues (see Section, On the Circulation in the Capillaries) have, however, opened out a large field for investigation of their probable functions in connection with the nutrition of the textures, in which, even in health, they appear to wander.

Under certain conditions, the red corpuscles pass through the walls of the capillaries (diapedesis), but these movements are probably passive, in other words, the cells are squeezed through the capillary wall, and do not, like the colourless cells, work their way through.

In both cases alike, no breach of surface occurs (p. 199).

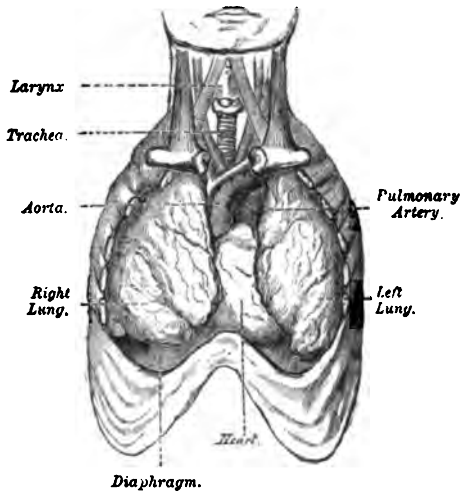
CHAPTER VII.

CIRCULATION OF THE BLOOD.

In the living body the contents of the chest,—the heart and lungs,—are the subjects of constant rhythmic movement, the result of which is an unceasing stream of air through the trachea alternately into and out of the lungs, and an unceasing stream of blood through the large arteries and veins, into and out of the heart.

It is with this last event that we are concerned especially in this chapter,—with the means, that is to say, by which the blood,

*Fig. 71.**



which at one moment is forced out of the heart, is in a few moments more returned to it, again to depart, and again pass through the body in course of what is technically called the

* Fig. 71. View of heart and lungs *in situ*. The front portion of the chest-wall, and the outer or *parietal* layers of the pleuræ and pericardium have been removed. The lungs are partly collapsed.

circulation. The puposes for which this unceasing current is maintained, are indicated in the uses of the blood enumerated in the preceding chapter.

The blood is conveyed away from the heart by the *arteries*, and returned to it by the *veins*; the arteries and veins being continuous with each other, at one end by means of the heart, and at the other by a fine network of vessels called the *capillaries*. The blood, therefore, in its passage from the heart passes first into the arteries, then into the capillaries, and lastly into the veins, by which it is conveyed back again to the heart,—thus completing a revolution, or *circulation*.

Fig. 72.*

As generally described there are *two* circulations by which all the blood must pass; the one, a shorter circuit from the heart to the lungs and back again; the other and larger circuit, from the heart to all parts of the body and back again; but more strictly speaking, there is only *one* complete circulation, which may be diagrammatically represented by a double loop, as in the accompanying figure (fig. 72).

On reference to this figure and noticing the direction of the arrows which represent the course of the stream of blood, it will be observed that while there is a smaller and a

* Fig. 72. Diagram of the circulation.

larger circle, both of which pass through the heart, yet that these are not distinct, one from the other, but are formed really by one continuous stream, the whole of which must, at one part of its course, pass through the lungs. Subordinate to the two principal circulations, the *pulmonary* and *systemic* as they are named, it will be noticed also in the same figure, that there is another, by which a portion of the stream of blood having been diverted once into the capillaries of the intestinal canal, and some other organs, and gathered up again into a single stream, is a second time divided in its passage through the liver, before it finally reaches the heart and completes a revolution. This subordinate stream through the liver is called the *portal* circulation.

Discovery of the Circulation.

It appears almost incredible that though anatomy had been studied for many centuries, and though such facts as the jetting of blood from a wounded artery, and the swelling up of veins on the distal side of a ligature, had long been noticed, the real course of the circulation remained unknown till the early part of the seventeenth century. The ignorance which so long prevailed is to be ascribed to the fact that men were content to take the assertions of their predecessors for granted, without bringing them to the test of observation.

Up to nearly the close of the sixteenth century it was generally believed that the blood passed from one ventricle to the other through foramina in the "septum ventriculorum." These foramina are of course purely imaginary, but no one ventured to dispute their existence till Servetus boldly stated that he could not succeed in finding them. He further asserted that the blood passed from the Right to the Left side of the heart by way of the lungs, and also advanced the hypothesis that it is thus "revivified," remarking that the Pulmonary Artery is too large to serve merely for the nutrition of the lungs (a theory then generally accepted).

Realdus, Columbo, and Cæsalpinus, added several important observations. The latter showed that the blood is slightly cooled by passing through the lungs, also that the veins swell up on the distal side of a ligature. The existence of valves in the veins had previously been discovered by *Fabricius of Aquapendente*, the teacher of Harvey.

The honour of first demonstrating the general course of the circulation belongs by right to Harvey, who made his grand discovery about 1618. He was the first to establish the muscular structure of the heart, which had been denied by many of his predecessors; and by careful study of its action both in the body and when excised, ascertained the order of contraction of its cavities. He did not content himself with inferences from the anatomy of the parts, but employed the experimental method of injection, and made an extensive and accurate series of observations on the circulation in cold blooded animals. He forced water through the Pulmonary Artery till it

trickled out through the Left ventricle, the tip of which had been cut off. Another of his experiments was to fill the Right side of the heart with water, tie the Pulmonary Artery and the Venæ Cavæ, and then squeeze the Right ventricle: not a drop could be forced through into the Left ventricle, and thus he conclusively disproved the existence of foramina in the septum ventriculorum. "I have sufficiently proved," says he, "that by the beating of the heart the blood passes from the veins into the arteries through the ventricles, and is distributed over the whole body."

"In the warmer animals, such as man, the blood passes from the Right Ventricle of the Heart through the Pulmonary Artery into the Lungs, and thence through the Pulmonary Veins into the Left Auricle, thence into the Left Ventricle."

The following are the main arguments by which he established the fact of the circulation :—

1. The heart in half an hour propels more blood than the whole mass of blood in the body.

2. The great force and jetting manner with which the blood spurts from an opened artery, such as the carotid, with every beat of the heart.

3. If true, the normal course of the circulation explains why after death the arteries are commonly found empty and the veins full.

4. If the large *veins* near the heart were tied in a fish or snake, the heart became pale, flaccid, and bloodless; on removing the ligature the blood again flowed into the heart. If the *artery* were tied, the heart became distended; the distension lasting until the ligature was removed.

5. The evidence to be derived from a ligature round a limb. If it be drawn very tight, no blood can enter the limb, and it becomes pale and cold. If the ligature be somewhat relaxed, blood can enter but cannot leave the limb; hence it becomes swollen and congested. If the ligature be removed, the limb soon regains its natural appearance.

6. The existence of valves in the veins which only permit the blood to flow towards the heart.

7. The general constitutional disturbance resulting from the introduction of a poison at a single point, *e.g.* snake poison.

To these may now be added many further proofs which have accumulated since the time of Harvey, *e.g.* :—

8. Wounds of arteries and veins. In the former case hæmorrhage may be almost stopped by pressure above, in the latter by pressure below, the seat of injury.

9. The direct observation of the passage of blood corpuscles from small arteries through capillaries into veins in all transparent vascular parts, as the mesentery, tongue or web of the frog, the tail or gills of a tadpole, &c.

10. The results of injecting certain substances into the blood. (See Hering's Experiments, p. 210.)

Further, it is obvious that the mere fact of the existence of a hollow muscular organ (the heart) with valves so arranged as to permit the blood to pass only in one direction, of itself suggests the course of the circulation. The only part of the circulation which Harvey could not follow is that through the capillaries, for the simple reason that he had no lenses sufficiently powerful to enable him to see it. *Malpighi* (1661) and *Leeuwenhoek* (1668) demonstrated it in the tail of the tadpole and lung of the frog.

The discovery of the circulation of the blood by Harvey forms the basis of modern physiology. His great treatise, "De Motu Cordis et Sanguinis," is a very model of accurate reasoning, based on a vast array of facts established by careful dissections and experiments, and collected from clinical observation. The conclusion at which he arrived is as follows:—"Since both by reasoning and by experiment the following facts have been established, viz., that the blood is forced through the lungs by the contraction of the ventricles, and is driven through the whole body where it traverses "porosities" in the flesh, and flows from the circumference towards the centre from the smaller into the larger veins, and thence into the vena cava and auricle, we cannot but conclude that in animals the blood moves in a circuit, and that this is the action or function of the heart which it accomplishes by its pulsations."

The principal force provided for constantly moving the blood through the course of the circulation is that of the muscular substance of the heart; other assistant forces are (2) those of the elastic walls of the arteries, (3) the pressure of the muscles among which some of the veins run, (4) the movements of the walls of the chest in respiration, and probably, to some extent, (5), the interchange of relations between the blood and the tissues which ensues in the capillary system during the nutritive processes. The right direction of the blood's course is determined and maintained by the valves of the heart to be immediately described; which valves open to permit the movement of the blood in the course described, but close when any force tends to move it in the contrary direction.

The Heart.

The heart is a hollow muscular organ, the interior of which is divided by a partition in such a manner as to form two chief chambers or cavities—right and left. Each of these chambers is again subdivided into an upper and a lower portion called respectively the *auricle* and *ventricle*, which freely communicate one with the other; the aperture of communication, however, being guarded by valvular curtains, so disposed as to allow blood to pass freely from the auricle into the ventricle, but not in the opposite direction. There are thus four cavities altogether in the heart—two auricles and two ventricles; the auricle and ventricle of one side being quite separate from those of the other (fig. 72).

The walls of the heart are constructed almost entirely of layers of muscular fibres; but a ring of connective tissue, to which some of the muscular fibres are attached, is inserted between each auricle and ventricle, and forms the boundary of the *auriculo-ventricular* opening. Fibrous tissue also exists at the origins of the pulmonary artery and aorta.

The muscular fibres of each auricle are in part continuous with those of the other, and partly separate; and the same remark holds true for the ventricles. The fibres of the auricles are, however, quite separate from those of the ventricles, the bond of connection between them being the fibrous tissue of the auriculo-ventricular openings.

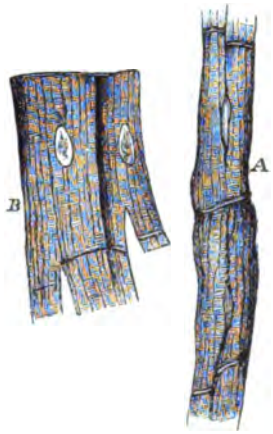
The walls of the left ventricle, which are nearly half-an-inch in thickness, are twice or three times as thick as those of the right. The left auricle is only slightly thicker than the right, the difference being as 1½ lines to 1 line. (Bouillaud.)

The average weight of the heart in the adult is from 9 to 10 ounces; its weight gradually increasing throughout life until it again diminishes by senile atrophy.

The heart is clothed on the outside by a thin transparent layer of *pericardium*, while its cavities are lined by a smooth and shining membrane, or

Fig. 73.*

Fig. 74.†



endocardium, which is directly continuous with the internal lining of the arteries and veins. The endocardium is composed of connective tissue,

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* Fig. 73. Muscular fibres from the heart, magnified, showing their cross-striæ, divisions and junctions (Kölliker).

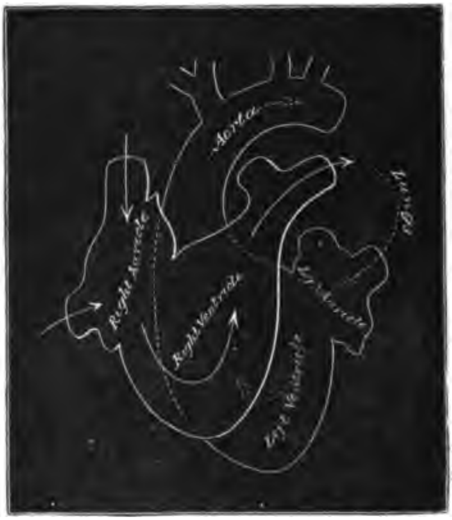
† Fig. 74. A. Muscular fibres from the heart of man, divided by transverse septa into separate nucleated portions. B. Two laterally adherent muscle-cells from the guinea-pig (Schweigger-Seidel).

with a large admixture of elastic fibres, and on its inner surface is laid down a single tessellated layer of flattened epithelial (endothelial) cells. Here and there muscular fibres are sometimes found in the tissue of the endocardium.

The muscular fibres of the heart, unlike those of other involuntary muscles, are striated; but although, in this respect, they resemble the voluntary muscles, they have distinguishing characteristics of their own. Each fibre is made up of a series of elongated nucleated cells (fig. 74), and the fibres which lie side by side are united at frequent intervals by short outgrowths from some of these cells. The fibres are smaller than those of the voluntary muscles, and their striation is less marked. No sarcolemma can be usually discerned.

The arrangement of the heart's valves is such that the blood can pass only in one direction, and this is as follows (fig. 75):—

Fig. 75.*



From the right auricle the blood passes into the right ventricle, and thence into the pulmonary artery, by which it is conveyed to the capillaries of the lungs. From the lungs the blood, which is now purified and altered in colour, is gathered by the pulmonary veins and taken to the left auricle. From the left

* Fig. 75. Diagram of the circulation through the heart (Dalton).

auricle it passes into the left ventricle, and thence into the aorta, by which it is distributed to the capillaries of every portion of the body. The branches of the aorta, from being distributed to the general system, are called *systemic* arteries; and from these the blood passes into the *systemic* capillaries, where it again becomes dark and impure, and thence into the branches of the *systemic* veins, which, forming by their union two large trunks, called the superior and inferior vena cava, discharge their contents into the right auricle, whence we supposed the blood to start (fig. 75).

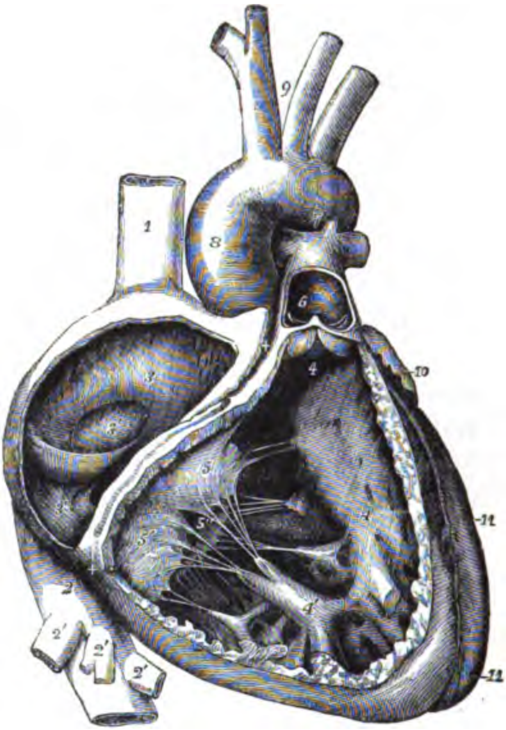
Structure of the Valves of the Heart.

The valves of the heart are formed essentially of thick layers of closely woven connective and elastic tissue, over which, on every part, is reflected the epithelial lining of the endocardium.

There are two sets of valves in the interior of the heart on each side (*a*) *auriculo ventricular*, between the auricle and ventricle (figs. 76, 5 and 77, 6), and (*b*) the *semilunar* or *arterial*, which are placed at the orifices respectively of the pulmonary artery and the aorta (figs. 76, 4 and 77, 7).

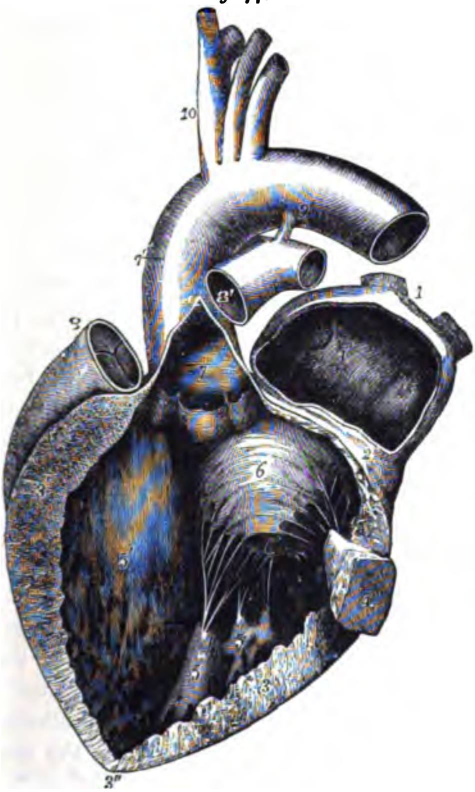
The valve between the right auricle and ventricle is named *tricuspid* (5, fig. 76), because it presents three principal cusps or subdivisions, and that between the left auricle and ventricle *bicuspid* or *mitral*, because it has two such portions (6, fig. 77). But in both valves there is between each two principal portions a smaller one; so that more properly, the tricuspid may be described as consisting of six, and the mitral of four, portions. Each portion is of triangular form, its apex and sides lying free in the cavity of the ventricle, and its base, which is continuous with the bases of the neighbouring portions, so as to form an annular membrane around the auriculo-ventricular opening, being fixed to a tendinous ring which encircles the orifice between the auricle and ventricle and receives the insertions of the muscular fibres of both. In each principal cusp may be distinguished a middle-piece, extending from its base to its apex, and including about half its width, which is thicker, and much tougher and tighter than the border-pieces or edges.

*Fig. 76.**



* Fig. 76. The right auricle and ventricle opened, and a part of their right and anterior walls removed, so as to show their interior. ½.—1, superior vena cava; 2, inferior vena cava; 2', hepatic veins cut short; 3, right auricle; 3', placed in the fossa ovalis, below which is the Eustachian valve; 3'', is placed close to the aperture of the coronary vein; +, +, placed in the auriculo-ventricular groove, where a narrow portion of the adjacent walls of the auricle and ventricle has been preserved; 4, 4, cavity of the right ventricle, the upper figure is immediately below the semilunar valves; 4', large columna carnea or musculus papillaris; 5, 5', 5'', tricuspid valve; 6, placed in the interior of the pulmonary artery, a part of the anterior wall of that vessel having been removed, and a narrow portion of it preserved at its commencement, where the semilunar valves are attached; 7, concavity of the aortic arch close to the cord of the ductus arteriosus; 8, ascending part or sinus of the arch covered at its commencement by the auricular appendix and pulmonary artery; 9, placed between the innominate and left carotid arteries; 10, appendix of the left auricle; 11, 11, the outside of the left ventricle, the lower figure near the apex (Allen Thomson).

Fig. 77.



* Fig. 77. The left auricle and ventricle opened and a part of their anterior and left walls removed so as to show their interior. ½.—The pulmonary artery has been divided at its commencement so as to show the aorta; the opening into the left ventricle has been carried a short distance into the aorta between two of the segments of the semilunar valves; the left part of the auricle with its appendix has been removed. The right auricle has been thrown out of view. 1, the two right pulmonary veins cut short; their openings are seen within the auricle; 1′, placed within the cavity of the auricle on the left side of the septum and on the part which forms th remains of the valve of the foramen ovale, of which the crescentic fold is seen towards the left hand of 1′; 2, a narrow portion of the wall of the auricle and ventricle preserved round the auriculo-ventricular orifice; 3, 3′, the cut surface of the walls of the ventricle, seen to become very much thinner towards 3″, at the apex; 4, a small part of the anterior wall of the left ventricle which has been preserved with the principal anterior columna carnea or musculus papillaris

While the bases of the several portions of the valves are fixed to the tendinous rings, their ventricular surfaces and borders are fastened by slender tendinous fibres, the *chordæ tendineæ*, to the walls of the ventricles, the muscular fibres of which project into the ventricular cavity in the form of bundles or columns—the *columnæ carneæ*. These columns are not all of them alike, for while some of them are attached along their whole length on one side, and by their extremities, others are attached only by their extremities; and a third set, to which the name *musculi papillares* has been given, are attached to the wall of the ventricle by one extremity only, the other projecting, papilla-like, into the cavity of the ventricle (5, fig. 77), and having attached to it *chordæ tendineæ*. Of the tendinous cords, besides those which pass from the walls of the ventricle and the *musculi papillares* to the margins of the valves both free and attached, there are some of especial strength, which pass from the same parts to the edges of the middle and thicker portions of the cusps before referred to (p. 141). The ends of these cords are spread out in the substance of the valve, giving its middle piece its peculiar strength and toughness; and from the sides numerous other more slender and branching cords are given off, which are attached all over the ventricular surface of the adjacent border-pieces of the principal portions of the valves, as well as to those smaller portions which have been mentioned as lying between each two principal ones. Moreover, the *musculi papillares* are so placed that, from the summit of each, tendinous cords may proceed to the adjacent halves of two of the principal divisions, and to one intermediate or smaller division, of the valve.

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attached to it; 5, 5, musculi papillares; 5′, the left side of the septum, between the two ventricles, within the cavity of the left ventricle; 6, 6′, the mitral valve; 7, placed in the interior of the aorta near its commencement and above the three segments of its semilunar valve which are hanging loosely together; 7′, the exterior of the great aortic sinus; 8, the root of the pulmonary artery and its semilunar valves; 8′, the separated portion of the pulmonary artery remaining attached to the aorta by 9, the cord of the ductus arteriosus; 10, the arteries rising from the summit of the aortic arch (Allen Thomson).

The preceding description applies equally to the mitral and tricuspid valve; but it should be added that the mitral is considerably thicker and stronger than the tricuspid, in accordance with the greater force which it is called upon to bear.

It has been already said that while the ventricles communicate, on the one hand, with the auricles, they communicate, on the other, with the large arteries which convey the blood away from the heart; the right ventricle with the pulmonary artery (6, fig. 76), which conveys blood to the lungs, and the left ventricle with the aorta, which distributes it to the general system (7, fig. 77). And as the auriculo-ventricular orifice is guarded by valves, so are also the mouths of the pulmonary artery and aorta (figs. 76, 77).

The valves, three in number, which guard the orifice of each of these two arteries, are called the *semilunar* valves. They are, like the auriculo-ventricular valves, constructed of fibrous and elastic tissue, over which is reflected the epithelium of the endocardium; and they are nearly alike on both sides of the heart; but those of the aorta are altogether thicker and more strongly constructed than those of the pulmonary artery, in accordance with the greater pressure which they have to withstand. Each valve is of semilunar shape, its convex margin being attached to a fibrous ring at the place of junction of the artery to the ventricle, and the concave or nearly straight border being free, so that each valve forms a little pouch like a watch-pocket (7, fig. 77). In the centre of the free edge of the valve, which contains a fine cord of fibrous tissue, is a small fibrous nodule, the *corpus Arantii*, and from this and from the attached border, fine fibres extend into every part of the mid substance of the valve, except a small lunated space just within the free edge, on each side of the *corpus Arantii*. Here the valve is thinnest, and composed of little more than the endocardium. Thus constructed and attached, the three semilunar valves are placed side by side around the arterial orifice of each ventricle, so as to form three little pouches, which can be thrown back and flattened by the blood passing out of the ventricle, but which belly out immediately so as to prevent any return (6, fig. 76). This will be again referred to immediately.

THE ACTION OF THE HEART.

The heart's action in propelling the blood consists in the successive alternate contractions and dilatations of the muscular walls of its two auricles and two ventricles; the auricles contracting simultaneously, and their contraction being immediately followed by that of the ventricles.

The description of the action of the heart may best be commenced at that period in each action which immediately precedes the beat of the heart against the side of the chest. For at this time the whole heart is in a passive state, the walls of both auricles and ventricles are relaxed, and their cavities are being dilated. The auricles are gradually filling with blood flowing into them from the veins; and a portion of this blood passes at once through them into the ventricles, the opening between the cavity of each auricle and that of its corresponding ventricle being, during all the *pause*, free and patent (fig. 78). The auricles, however, receiving more blood than at once passes through them to the ventricles, become, near the end of the pause, fully distended; then, at the end of the pause, they contract and expel their contents into the ventricles. The contraction of the auricles is sudden and very quick; it commences at the entrance of the great veins into them, and is thence propagated towards the auriculo-ventricular opening; but the last part which contracts is the auricular appendix. The effect of this contraction

Fig. 78.*

* Fig. 78. Diagram of valves of the heart (after Dalton).

of the auricles is to quicken the flow of blood from them into the ventricles; the force of their contraction not being sufficient under ordinary circumstances to cause any back-flow into the veins. The reflux of blood into the great veins is indeed resisted not only by the mass of blood in the veins and the force with which it streams into the auricles, but also by the simultaneous contraction of the muscular coats with which the large veins are provided near their entrance into the auricles. Any slight regurgitation from the right auricle is limited also by the valves at the junction of the subclavian and internal jugular veins, beyond which the blood cannot move backwards; and the coronary vein, or vein which brings back to the right auricle the blood which has circulated in the substance of the heart, is preserved from it by a valve at its mouth.

In birds and reptiles, regurgitation from the right auricle is prevented by valves placed at the entrance of the great veins.

During the auricular contraction, the force of the blood propelled into the ventricle is transmitted in all directions, but being insufficient to separate the semilunar valves, it is expended in distending the ventricle, and in raising and gradually closing the auriculo-ventricular valves, which, when the ventricle is full, form a complete septum between it and the auricle. This elevation of the auriculo-ventricular valves is, no doubt, materially aided by the action of the elastic tissue which Dr. Markham has shown to exist so largely in their structure, especially on the auricular surface.

The blood which is thus driven, by the contraction of the auricles, into the corresponding ventricles, being added to that which had already flowed into them during the heart's pause, is sufficient to complete the dilatation or diastole of the ventricles. Thus distended, they immediately contract: so immediately, indeed, that their contraction, or systole, looks as if it were continuous with that of the auricles. This has been graphically described by Harvey in the following passage:—"These two motions, one of the ventricles, another of the auricles, take place consecutively, but in such a manner that there is a kind of

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harmony, or rhythm, present between them, the two concurring in such wise that but one motion is apparent; especially in the warmer blooded animals, in which the movements in question are rapid. Nor is this for any other reason than it is in a piece of machinery, in which, though one wheel gives motion to another, yet all the wheels seem to move simultaneously; or in that mechanical contrivance which is adapted to fire-arms, where the trigger being touched, down comes the flint, strikes against the steel, elicits a spark, which, falling among the powder, it is ignited, upon which the flame extends, enters the barrel, causes the explosion, propels the ball, and the mark is attained—all of which incidents by reason of the celerity with which they happen, seem to take place in the twinkling of an eye." The ventricles contract much more slowly than the auricles, and in their contraction, probably always thoroughly empty themselves, differing in this respect from the auricles, in which, even after their complete contraction, a small quantity of blood remains. The form and position of the fleshy columns on the internal walls of the ventricle appear, indeed, especially adapted to produce this obliteration of their cavities during their contraction; and the completeness of the closure may often be observed on making a transverse section of a heart shortly after death, in any case in which the contraction of the *rigor mortis* is very marked (fig. 79). In such a case, only a central fissure may be discernible to the eye in the place of the cavity of each ventricle.

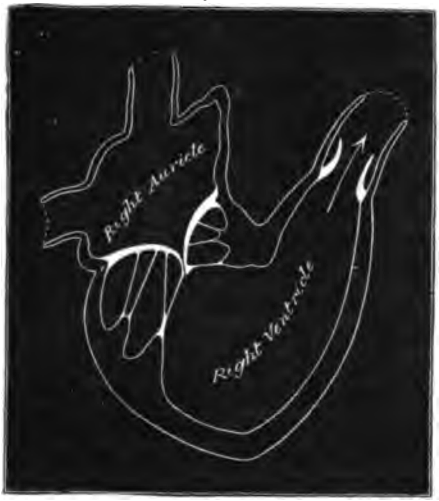
*Fig. 79.**

When the ventricles contract on the blood contained in them, the pressure is transmitted equally to all parts of their internal surface, including the ventricular surface of both sets of valves, (auriculo-ventricular and semilunar). The effect, respectively, on the two sets of valves is quite different. The

* Fig. 79. Transverse section of bullock's heart in a state of cadaveric rigidity. *a*, cavity of left ventricle. *b*, cavity of right ventricle. (Dalton.)

auriculo-ventricular valves which have been floated upwards on the surface of the in-streaming blood,—like the leaves of a water-plant, as Dr. Pettigrew happily expresses it,—are, by the pressure on the blood of the contracting ventricle now stretched tightly and pressed more closely together (fig. 80), so as to offer an impassable barrier against the return of blood into the auricle; the margins of the cusps being still more secured in apposition, one with another, by the simultaneous contraction of the *musculi papillares*, whose chordæ tendineæ have a special mode of attachment for this object (p. 144).

Fig. 80.*



The *semilunar* valves, on the other hand, which are closed in the intervals of the ventricle's contraction (fig. 78), are forced apart by the same pressure that tightens the auriculo-ventricular valves; and, thus, the whole force of the contracting ventricles is directed to the expulsion of blood through the aorta and pulmonary artery (fig. 80).

A special advantage derived from the action of the *musculi papillares* is that they prevent the auriculo-ventricular valves from being everted into the auricle. For, as the heart shortens itself in contraction, the *chordæ tendineæ* might allow the valves to be pressed back into the auricle, were it not that when the wall of the ventricle is drawn nearer to the auriculo-ventricular orifice, the *musculi papillares* more than compensate for this by

* Fig. 80. Diagram of valves of the heart (after Dalton).

their own contraction—holding the cords tight, and, by pulling down the valves, adding slightly to the force with which the blood is expelled.

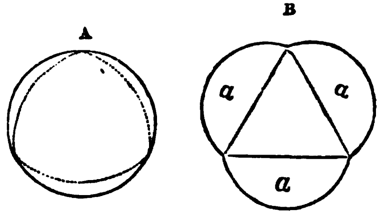
Thus, the ventricle, in its contraction, may be compared to a conical or funnel-shaped room of which the sides, floor, and roof are all drawn towards a central line for the more complete expulsion of its contents.

What has been said applies equally to the auriculo-ventricular valves on both sides of the heart, and of both alike the closure is generally complete every time the ventricles contract. But in some circumstances the closure of the tricuspid valve is not complete, and a certain quantity of blood is forced back into the auricle. This has been called the *safety-valve action* of this valve (Hunter, Wilkinson King). The circumstances in which it usually happens are those in which the vessels of the lung are already full enough when the right ventricle contracts, as *e.g.*, in certain pulmonary diseases, in very active exertion, and in great efforts. In these cases, the tricuspid valve does not completely close, and the regurgitation of blood may be indicated by a pulsation in the jugular veins synchronous with that in the carotid arteries.

The *arterial* or *semilunar* valves are, as already said, forced apart by the out-streaming blood, with which the contracting ventricle dilates the large arteries. The dilatation of the arteries is, in a peculiar manner, adapted to bring the valves into action. The lower borders of the semilunar valves are attached to the inner surface of a tendinous ring, which is, as it were, inlaid, at the orifice of the artery, between the muscular fibres of the ventricle and the elastic fibres of the walls of the artery. The tissue of this ring is tough, and does not admit of extension under such pressure as it is commonly exposed to; the valves are equally inextensile, being, as already mentioned, formed of tough, close-textured, fibrous tissue, with strong interwoven cords, and covered with *endocardium*. Hence, when the ventricle propels blood through the orifice and into the canal of the artery, the lateral pressure which it exercises is sufficient to dilate the walls of the artery, but not enough to stretch in an equal degree, if at

all the unyielding valves and the ring to which their lower borders are attached. The effect, therefore, of each such propulsion of blood from the ventricle is, that the wall of the first portion of the artery is dilated into three pouches behind the valves, while the free margins of the valves, which had previously lain in contact with the inner surface of the artery (as at A, fig. 81), are drawn inward towards its centre (fig. 81, B). Their positions may be explained by the foregoing diagrams, in which the continuous lines represent a transverse section of the arterial walls, the dotted one the edges of the valves, firstly, when the valves are in contact with the walls (A), and, secondly, when the walls being dilated, the valves are drawn away from them (B).

Fig. 81.*



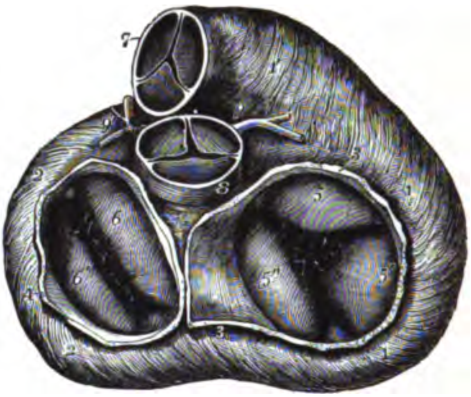
This position of the valves and arterial walls is retained so long as the ventricle continues in contraction: but, so soon as it relaxes, and the dilated arterial walls can recoil by their elasticity, they press the blood as well towards the ventricles as onwards in the course of the circulation. Part of the blood thus pressed back lies in the pouches (*a*, fig. 81, B) between the valves and the arterial walls; and the valves are by it pressed together till their thin lunated margins meet in three lines radiating from the centre to the circumference of the artery (7 and 8, fig. 82).

The contact of the valves in this position, and the complete closure of the arterial orifice, are secured by the peculiar construction of their borders before mentioned. Among the cords which are interwoven in the substance of the valves, are two of

* Fig. 81. Sections of aorta, to show the action of the semilunar valves. A is intended to show the valves, represented by the dotted lines, in contact with the arterial walls, represented by the continuous outer line. B (after Hunter) shows the arterial wall distended into three pouches (*a*), and drawn away from the valves which are straightened into the form of an equilateral triangle, as represented by the dotted lines.

greater strength and prominence than the rest; of which one extends along the free border of each valve, and the other forms a double curve or festoon just below the free border. Each of

Fig. 82.*



these cords is attached by its outer extremities to the outer end of the free margin of its valve, and in the middle to the corpus Arantii; they thus enclose a lunated space from a line to a line and a half in width, in which space the substance of the valve is much thinner and more pliant than elsewhere. When the valves are pressed down, all these parts or spaces of their surfaces come into contact, and the closure of the arterial orifice is thus secured by the apposition not of the mere edges of the valves, but of all

* Fig. 82. View of the base of the ventricular part of the heart, showing the relative position of the arterial and auriculo-ventricular orifices.—⅔. The muscular fibres of the ventricles are exposed by the removal of the pericardium, fat, blood-vessels, etc.; the pulmonary artery and aorta have been removed by a section made immediately beyond the attachment of the semilunar valves, and the auricles have been removed immediately above the auriculo-ventricular orifices. The semilunar and auriculo-ventricular valves are in the nearly closed condition. 1, 1, the base of the right ventricle; 1′, the conus arteriosus; 2, 2, the base of the left ventricle; 3, 3, the divided wall of the right auricle; 4, that of the left; 5, 5′, 5″, the tricuspid valve; 6, 6′, the mitral valve. In the angles between these segments are seen the smaller fringes frequently observed; 7, the anterior part of the pulmonary artery; 8, placed upon the posterior part of the root of the aorta; 9, the right, 9′, the left coronary artery. (Allen Thomson).

those thin lunated parts of each which lie between the free edges and the cords next below them. These parts are firmly pressed together, and the greater the pressure that falls on them the closer and more secure is their apposition. The corpora Arantii meet at the centre of the arterial orifice when the valves are down, and they probably assist in the closure; but they are not essential to it, for, not unfrequently, they are wanting in the valves of the pulmonary artery, which are then extended in larger, thin, flapping margins. In valves of this form, also, the inlaid cords are less distinct than in those with corpora Arantii; yet the closure by contact of their surfaces is not less secure.

Mr. Savory has clearly shown that this pressure of the blood is not entirely sustained by the valves alone, but in part by the muscular substance of the ventricle. Availing himself of a method of dissection hitherto apparently overlooked, namely, that of making vertical sections (fig. 83) through various parts of the tendinous rings, he has been enabled to show clearly that the aorta and pulmonary artery, expanding towards their termination, are situated upon the *outer* edge of the thick upper border of the ventricles, and that consequently the portion of each semilunar valve adjacent to the vessel passes over and rests upon the muscular substance—being thus supported, as it were, on a kind of muscular floor formed by the upper border of the ventricle. The result of this arrangement will be that the reflux of the blood will be most efficiently sustained by the ventricular wall.†

Fig. 83.*

As soon as the auricles have completed their contraction they begin again to dilate, and to be refilled with blood, which flows into them in a steady stream

* Fig. 83. Vertical section through the aorta at its junction with the left ventricle. *a*, Section of aorta. *b*, Section of valve. *c*, Section of wall o ventricle. *d*, Internal surface of ventricle.

† Mr. Savory's preparations, illustrating this and other points in relation to the structure and functions of the valves of the heart, are in the museum of St. Bartholomew's Hospital.

through the great venous trunks. They are thus filling during all the time in which the ventricles are contracting; and the contraction of the ventricles being ended, these also again dilate, and receive again the blood that flows into them from the auricles. By the time that the ventricles are thus from one-third to two-thirds full, the auricles are distended; these, then suddenly contracting, fill up the ventricles, as already described, p. 146.

If we suppose a cardiac revolution, which includes the contraction of the auricles, the contraction of the ventricles, and their repose, to occupy rather more than a second, the following table will represent, in tenths of a second, the time occupied by the various events we have considered.

Contraction of Auricles . . .	1 +	Repose of Auricles . . .	10=11
" Ventricles . .	4 +	" Ventricles . .	7=11
Repose (no contraction of either auricles or ventricles) . . .	6 +	Contraction (of either auricles or ventricles) . . .	5=11
	— 11		

If the speed of the heart be quickened, the time occupied by each cardiac revolution is of course diminished, but the diminution affects only the diastole and pause. The systole of the ventricles occupies very much the same time, about $\frac{4}{10}$ sec., whatever the pulse-rate.

The periods in which the several valves of the heart are in action may be connected with the foregoing table; for the auriculo-ventricular valves are closed, and the arterial valves are open during the whole time of the ventricular contraction, while, during the dilatation and distension of the ventricles the latter valves are shut, the former open.

Sounds of the Heart.

When the ear is placed over the region of the heart, two *sounds* may be heard at every beat of the heart, which follow in quick succession, and are succeeded by a *pause* or period of silence. The *first* sound is dull and prolonged; its commencement coincides with the impulse of the heart, and just precedes the pulse at the wrist. The *second* is a shorter and sharper

sound, with a somewhat flapping character, and follows close after the arterial pulse. The period of time occupied respectively by the two sounds taken together, and by the pause, are almost exactly equal. The relative length of time occupied by each sound, as compared with the other, is a little uncertain. The difference may be best appreciated by considering the different forces concerned in the production of the two sounds. In one case there is a strong, comparatively slow, contraction of a large mass of muscular fibres, urging forward a certain quantity of fluid against considerable resistance; while in the other it is a strong but shorter and sharper recoil of the elastic coat of the large arteries,—shorter because there is no resistance to the flapping back of the semilunar valves, as there was to their opening. The difference may be also expressed, as Dr. C. J. B. Williams has remarked, by saying the words *lūbb—dŭp*.

The events which correspond, in point of time, with the *first* sound, are the contraction of the ventricles, the first part of the dilatation of the auricles, the closure of the auriculo-ventricular valves, the opening of the semilunar valves, and the propulsion of blood into the arteries. The sound is succeeded, in about one-thirtieth of a second, by the pulsation of the facial artery, and in about one-sixth of a second, by the pulsation of the arteries at the wrist. The *second* sound, in point of time, immediately follows the cessation of the ventricular contraction, and corresponds with the closure of the semilunar valves, the continued dilatation of the auricles, the commencing dilatation of the ventricles, and the opening of the auriculo-ventricular valves. The *pause* immediately follows the second sound, and corresponds in its first part with the completed distension of the auricles, and in its second with their contraction, and the distension of the ventricles, the auriculo-ventricular valves being, all the time of the pause, open, and the arterial valves closed.

The chief cause of the first sound of the heart appears to be the vibration of the auriculo-ventricular valves, and also, but to a less extent, of the ventricular walls, and coats of the aorta and pulmonary artery, all of which parts are suddenly put into a state of tension at the moment of ventricular contraction. The

effect is intensified by the *muscular sound* produced by the contraction of the mass of muscular fibres which form the ventricle.

This view, long ago advanced by Dr. Billing, is supported by the fact observed by Valentin, that if a portion of a horse's intestine, tied at one end, be moderately filled with water, without any admixture of air, and have a syringe containing water fitted to the other end, the first sound of the heart is exactly imitated by forcing in more water, and thus suddenly rendering the walls of the intestine more tense.

The cause of the *second* sound is more simple than that of the first. It is probably due entirely to the sudden closure and consequent vibration of the semilunar valves when they are pressed down across the orifices of the aorta and pulmonary artery. The influence of the valves in producing the sound, is illustrated by the experiment already quoted from Valentin, and from others performed on large animals, such as calves, in which the results could be fully appreciated. In these experiments two delicate curved needles were inserted, one into the aorta, and another into the pulmonary artery, below the line of attachment of the semilunar valves, and, after being carried upwards about half an inch, were brought out again through the coats of the respective vessels, so that in each vessel one valve was included between the arterial walls and the wire. Upon applying the stethoscope to the vessels, after such an operation, the second sound had ceased to be audible. Disease of these valves, when so extensive as to interfere with their efficient action, also often demonstrates the same fact by modifying or destroying the distinctness of the second sound.

One reason for the second sound being a clearer and sharper one than the first may be, that the semilunar valves are not covered in by the thick layer of fibres composing the walls of the heart to such an extent as are the *auriculo-ventricular*. It might be expected therefore that their vibration would be more easily heard through a stethoscope applied to the walls of the chest.

The contraction of the auricles which takes place in the end of the pause is inaudible outside the chest, but may be heard, when the heart is exposed and the stethoscope placed on it, as a

slight sound preceding and continued into the louder sound of the ventricular contraction.

The Impulse of the Heart.—At the commencement of each ventricular contraction, the heart may be felt to beat with a slight shock or *impulse* against the walls of the chest. This impulse is most evident in the space between the fifth and sixth ribs, between one and two inches to the left of the sternum. The force of the impulse, and the extent to which it may be perceived beyond this point, vary considerably in different individuals, and in the same individuals under different circumstances. It is felt more distinctly, and over a larger extent of surface, in emaciated than in fat and robust persons, and more during a forced expiration than in a deep inspiration; for, in the one case, the intervention of a thick layer of fat or muscle between the heart and the surface of the chest, and in the other the inflation of the portion of lung which overlaps the heart, prevents the impulse from being fully transmitted to the surface. An excited action of the heart, and especially a hypertrophied condition of the ventricles, will increase the impulse, while a depressed condition, or an atrophied state of the ventricular walls, will diminish it.

The impulse of the heart is probably the result, in part, (*a*) of a tilting forwards of the apex, so that it is made to strike against the walls of the chest; this tilting movement being effected by the contraction of the spiral muscular fibres of the ventricles. The whole extent of the movement thus produced is, however, but slight. The condition, which, no doubt, contributes most to the occurrence and character of the impulse of the heart, is (*b*) its change of shape; for, during the contraction of the ventricles, and the consequent approximation of the base towards the apex, the heart becomes more globular, and bulges so much, that a distinct impulse is felt when the finger is placed over the bulging portion, either at the front of the chest, or under the diaphragm. The production of the impulse is, perhaps, further assisted by (*c*) the tendency of the aorta to straighten itself and diminish its curvature when distended with the blood impelled by the ventricle; and (*d*) by the elastic recoil of all the parts about the base of

the heart, which, according to the experiments of Kurschner, are stretched downward and backward by the blood flowing into the auricles and ventricles during the dilatation of the latter, but recover themselves when, at the beginning of the contraction of the ventricles, the flow through the auriculo-ventricular orifices is stopped. But these last-mentioned conditions can only be accessory in the perfect state of things; for the same tilting movement of the heart ensues when its apex is cut off, and when, therefore, no tension or change of form can be produced by the blood.

Although what we generally recognize as the impulse of the heart is produced in the way just mentioned, the beat is not so simple a shock as it may seem when only felt by the finger. By means of an instrument called a *cardiograph*, it may be shown to be compounded of three or four shocks, of which the finger can only feel the greatest.

Fig. 84.*

The *Cardiograph* (fig. 84) consists of a disc-shaped box (*b*), one side of which is formed of elastic membrane; and in connection with the latter is an ivory knob (A) for application to the chest-wall over the place of the greatest impulse of the heart. The box or *tympanum* communicates by means of an air-tight elastic tube (*f*) with the interior of a second tympanum (fig. 85, *b*),

Fig. 85.†

* Fig. 84. Dr. Burdon-Sanderson's Cardiograph.
† Fig. 85. Registering apparatus of Cardiograph.

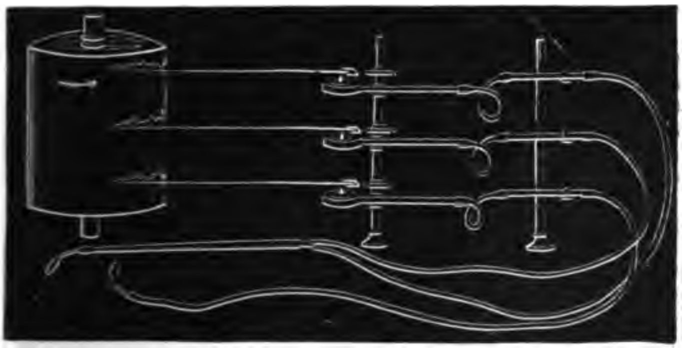
in connection with which is a long and light lever (*a*). The shock of the heart's impulse being communicated to the ivory knob, and through it to the first tympanum, the effect is, of course, at once transmitted by the column of air in the elastic tube to the interior of the second tympanum, also closed, and through the elastic and movable lid of the latter to the lever, which is placed in connection with a *registering* apparatus. (For explanation of *Registering apparatus* see figs. 87 and 102, with accompanying descriptions in the text.)

A *tracing* of the heart's impulse is thus obtained. (Fig. 86.)

Fig. 86.*

Its interpretation will be best understood by reference to Figs. 87 and 88, with the accompanying text.

Fig. 87.†



* Fig. 86. Tracing of heart's impulse of man (Marey).

† Fig. 87. Apparatus of MM. Chauveau and Marey for estimating the variations of endocardial pressure, and production of impulse of the heart.

By placing three small india-rubber air-bags in the interior respectively of the right auricle, the right ventricle, and in an intercostal space in front of the heart of living animals (horse), and placing these bags, by means of long narrow tubes, in communication with three levers, arranged one over the other in connection with a registering apparatus (fig. 87), MM. Chauveau and Marey have been able to measure with much accuracy the variations of the endocardial pressure and the comparative duration of the contractions of the auricles and ventricles. By means of the same apparatus, the synchronism of the impulse with the contraction of the ventricles, is also well shown; and the causes of the several vibrations of which it is really composed, have been discovered.

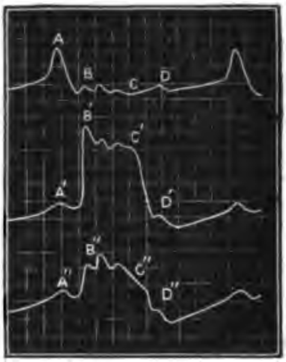
In the tracing (fig. 88), the intervals between the vertical lines represent periods of a tenth of a second. The parts on which any given vertical line

Fig. 88.*

1. Auricular tracing.

2. Ventricular tracing.

3. Impulse tracing.



falls represent, of course, simultaneous events. Thus,—it will be seen that the contraction of the auricle, indicated by the upheaval of the tracing at A in first tracing, causes a slight increase of pressure in the ventricle (A' in second tracing), and produces a tiny impulse (A" in third tracing). So also, the closure of the semilunar valves, while it causes a momentarily increased pressure in the ventricle at D', does not fail to affect the pressure in the auricle D, and to leave its mark in the tracing of the impulse also, D".

The large upheaval of the ventricular and the impulse tracings, between A' and D', and A" and D", are caused by the ventricular contraction, while the smaller undulations, between B and C, B' and C', B" and C", are caused by the vibrations consequent on the tightening and closure of the auriculo-ventricular valves.

* Fig. 88. Tracings obtained by Chauveau and Marey's apparatus (Fig. 87).

Frequency and Force of the Heart's Action.

The heart of a healthy adult man in the middle period of life, contracts from seventy to seventy-five times in a minute; but many circumstances cause this rate, which of course corresponds with that of the arterial *pulse* (p. 179), to vary even in health. The chief are age, temperament, sex, food and drink, exercise, time of day, posture, atmospheric pressure, temperature.

Age.—The frequency of the heart's action gradually diminishes from the commencement to near the end of life, but is said to rise again somewhat in extreme old age, thus:—

Before birth the average number of pulses in a minute is	150
Just after birth	from 140 to 130
During the first year	130 to 115
During the second year	115 to 100
During the third year	100 to 90
About the seventh year	90 to 85
About the fourteenth year, the average number of pulses in a minute is from	85 to 80
In adult age	80 to 70
In old age	70 to 60
In decrepitude	75 to 65

Temperament and Sex.—In persons of sanguine temperament, the heart acts somewhat more frequently than in those of the phlegmatic; and in the female sex more frequently than in the male.

Food and Drink. Exercise.—After a meal its action is accelerated, and still more so during bodily exertion or mental excitement; it is slower during sleep.

Diurnal Variation.—From the observation of several experimenters, it appears that, in the state of health, the pulse is most frequent in the morning, and becomes gradually slower as the day advances: and that this diminution of frequency is both more regular and more rapid in the evening than in the morning.

Posture.—It is found that, as a general rule, the pulse, especially in the adult male, is more frequent in the standing than in the sitting posture, and in the latter than in the recumbent position; the difference being greatest between the standing and the sitting posture. The effect of change of posture is greater as the frequency of the pulse is greater, and, accordingly, is more marked in the morning than in the evening. Dr. Guy, by supporting the body in different postures, without the aid of muscular effort of the individual, has proved that the increased frequency of the pulse in the sitting and standing positions is dependent upon the muscular exertion engaged in maintaining them; the usual effect of these postures on the

pulse being almost entirely prevented when the usually attendant muscular exertion was rendered unnecessary.

Atmospheric Pressure.—According to Parrot, the frequency of the pulse increases in a corresponding ratio with the elevation above the sea; and Dr. Frankland informed the author, that at the summit of Mont Blanc his pulse was about double its ordinary rate. After six hours' perfect rest and sleep at the top, it was 120, on descending to the corridor it fell to 108, at the Grands Mulets it was 88, at Chamounix 56; normally, his pulse is 60.

Temperature.—The rapidity and force of the heart's contractions are largely influenced by variations of temperature. The frog's heart, when excised, ceases to beat if the temperature be reduced to 32°. When heat is gradually applied to it, both the speed and force of the heart's contractions increase till they reach a maximum. If the temperature is still further raised the beats become irregular and feeble, and the heart at length stands still in a condition of "heat rigor."

Similar effects are produced in warm-blooded animals. In the rabbit, Dr. Brunton found that the number of heart-beats was more than doubled when the temperature of the air was maintained at 105° F. At 113°—114° F. the rabbit's heart ceases to beat.

In health there is observed a nearly uniform relation between the frequency of the pulse and of the respirations; the proportion being, on an average, one of the latter to three or four of the former. The same relation is generally maintained in the cases in which the pulse is naturally accelerated, as after food or exercise; but in disease this relation usually ceases to exist. In many affections accompanied with increased frequency of the pulse, the respiration is, indeed, also accelerated, yet the degree of its acceleration may bear no definite proportion to the increased number of the heart's actions: and in many other cases, the pulse becomes more frequent without any accompanying increase in the number of respirations; or, the respiration alone may be accelerated, the number of pulsations remaining stationary, or even falling below the ordinary standard.

The *force* with which the left ventricle of the heart contracts is about double that exerted by the contraction of the right: being equal (according to Valentin) to about $\frac{1}{50}$th of the weight of the whole body, that of the right being equal only to $\frac{1}{100}$th of the same. This difference in the amount of force exerted by the contraction of the two ventricles, results from the walls of the left ventricle being about twice as thick as those of the right. And the difference is adapted to the greater degree of resistance

which the left ventricle has to overcome, compared with that to be overcome by the right: the former having to propel blood through every part of the body, the latter only through the lungs.

The force exercised by the auricles in their contraction has not been determined. Neither is it known with what amount of force either the auricles or the ventricles dilate; but there is no evidence for the opinion, that in their dilatation they can materially assist the circulation by any such action as that of a sucking-pump, or a caoutchouc bag, in drawing blood into their cavities.

That the force which the ventricles exercise in dilatation is very slight, has been proved by Oesterreicher. He removed the heart of a frog from the body, and laid upon it a substance sufficiently heavy to press it flat, and yet so small as not to conceal the heart from view; he then observed that during the contraction of the heart, the weight was raised; but that during its dilatation, the heart remained flat. And the same was shown by Dr. Clendinning, who, applying the points of a pair of spring callipers to the heart of a live ass, found that their points were separated as often as the heart swelled up in the contraction of the ventricles, but approached each other by the force of the spring when the ventricles dilated. Seeing how slight the force exerted in the dilatation of the ventricles is, it has been supposed that they are only dilated by the pressure of the blood impelled from the auricles; but that both ventricles and auricles dilate spontaneously is proved by their continuing their successive contractions and dilatations when the heart is removed, or even when they are separated from one another, and when therefore no such force as the pressure of blood can be exercised to dilate them.

The *capacity* of the two ventricles is probably the same. It is difficult to determine with certainty how much this may be; but, taking the mean of various estimates, it may be inferred that each ventricle is able to contain on an average, about three ounces of blood, the whole of which is impelled into their respective arteries at each contraction. The capacity of the auricles is rather less than that of the ventricles: the thickness of their walls is considerably less. The latter condition is adapted to the small amount of force which the auricles require in order to empty themselves into their adjoining ventricles; the former to the circumstance of the ventricles being partly filled with blood before the auricles contract.

Work done by the Heart.—In estimating the work done by any machine it is usual to express it in terms of the "unit of work." The unit of work is defined to be the energy expended in raising a unit of weight (1 lb.) through a unit of height (1 ft.). In England, the unit of work is the "*foot-pound*," in France, the "*kilogrammetre*."

The work done by the heart at each contraction can be readily found by multiplying the weight of blood expelled by the ventricles by the height to which the blood rises in a tube tied into an artery. This height Dr. Hales found to be about 9 ft. in the horse, and Dr. Haughton has shown that his estimate is nearly correct for a large artery in man. Taking the weight of blood expelled from the left ventricle at each systole as 4 oz., *i.e.*, $\frac{1}{4}$lb., we have $9 \times \frac{1}{4} = 2\frac{1}{4}$ foot pounds as the work done by the left ventricle at each systole; and adding to this the work done by the right ventricle (about $\frac{1}{3}$ that of the left) we have $2\frac{1}{4} + \frac{3}{4} = 3$ foot pounds as the work done by the heart at each contraction. Other estimates give $\frac{1}{2}$ kilogrammetre, or about $3\frac{1}{2}$ foot pounds.

Dr. Haughton calculates that the total work of the heart in 24 hrs. is about 124 *foot tons*, and to give a more definite idea of this wonderful energy, exhibits it by contrast: "Let us suppose that the heart expends its entire force in lifting its own weight vertically, then the height through which it could lift itself in *one hour* is found to be 20,250 ft. (Helmholtz).

"It has been frequently stated that an active climber can ascend 9,000 feet in nine hours, which is only at the rate of 1,000 feet per hour, or $\frac{1}{20}$th part of the energy of the heart.

"When the railway was constructed from Trieste to Vienna, a prize was offered for the locomotive Alp-engine that could lift its own weight through the greatest height in one hour. The prize locomotive was the 'Bavaria,' which lifted herself through 2,700 feet in one hour: the greatest feat yet accomplished on steep gradients. This result, remarkable as it is, is only $\frac{1}{8}$th part of the energy of the human heart."

N.B. In making these comparisons we must not forget that the work done by the climber and the engine in foot pounds far exceeds that of the heart, though the height to which the heart would raise its *own* (small) weight is much greater than in the other two cases.

Influence of the Nervous System on the Action of the Heart.

The heart contains in its own walls microscopic ganglia or nerve-centres, and inter-communicating nerve-fibres, by which its action is immediately governed.

Under ordinary conditions, the contact of blood with the endocardium and the accompanying distension of the heart's cavities are the stimuli, which, by *reflex* action through these ganglia and nerve-fibres, excite the heart's contraction. The momentary exhaustion of the nerve and muscle-apparatus, which

of necessity follows the contraction, provides the condition of relaxation, under which the heart's cavities can be again distended by the in-flowing blood.

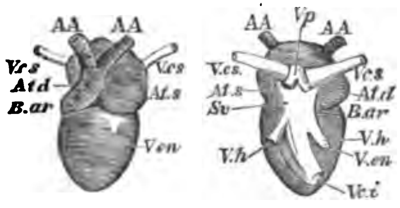
This alternation of contraction and dilatation, which is repeated at regular intervals of rather less than a second, is called the *rhythm* of the heart.

The functions of the microscopic ganglia present in the heart have been made the subject of physiological experiments only in cold-blooded animals. In the frog, ganglia (Remak's) lie in the wall of the sinus venosus; another ganglion (Bidder's) is situate near the junction of the auricles with the ventricle, and a third group of ganglionic corpuscles is situate in the septum between the two auricles.

There can be little doubt that these ganglia, or, at least, some of them, are the nerve-centres through which is reflected the stimulus which excites the heart's contraction; for when the heart is divided into two or more parts, only those parts which contain ganglionic corpuscles are capable of pulsating rhythmically.

When the heart is divided or ligatured at the line of junction of the *sinus venosus* with the right auricle, the sinus continues to pulsate, while the rest of the heart is, for a time, motionless: (Stannius.) although, after a time, it again begins to act; but its rhythm is now different from that of the sinus. If the ventricle be cut off from the auricles it will continue to pulsate; and its rhythmic pulsation will at once re-commence, if this be done during the time in which the heart is lying motionless on account of the separation, as just mentioned, of the sinus venosus.

Fig. 89.*



The heart's rhythmic contraction is, under ordinary circumstances, sufficiently intelligible, and is what might be expected of any muscle under analogous conditions of regularly repeated

* Fig. 89. Heart of frog (Burdon-Sanderson after Fritsche). Front view to the left, back view to the right. A A, *Aortæ.* V. c. s. *Venæ cavæ superiores.* At. s. *left auricle.* At. d. *right auricle.* Ven. *Ventricle.* B. ar. *Bulbus arteriosus.* S. v. *Sinus venosus.* V. c. i. *Vena cava inferior.* V. h. *Venæ hepaticæ.* V. p. *Venæ pulmonales.*

stimulation. It is less easy to understand the apparently strange phenomenon of continuance of rhythmic action in a heart which has been removed from the body—a phenomenon which, although lasting only for a minute or two in a warm-blooded animal, may continue for many hours in a cold-blooded, if the precautions as to temperature, moisture, and the presence of oxygen be observed.

The best interpretation yet given of it, and of rhythmic processes in general, is that by Sir James Paget, who regards them as dependent on *rhythmic nutrition*, *i.e.* on a method of nutrition in which, after the exhaustion produced by action, the acting parts are gradually raised, with time-regulated progress, to a certain state of instability of composition, which then issues in the discharge of their functions. Thus, in the present case, nerve-force issues, or is liberated from the cardiac ganglia, so soon as it reaches a certain degree of tension, and the effect of its transmission is the contraction of the muscular fibres to which branches from the ganglia are distributed, and whose irritability has been also simultaneously raised.

The comparative frequency of the heart's rhythmic movements depends on the original constitution of the parts concerned, and introduces no fresh difficulty in the way of understanding the matter. All muscles and nerve-centres have a tendency to rhythm, when there is uniformity in the stimulus which excites them to action. And the difficulty in comprehending the fact of the heart being 'set' to act sixty or seventy times in a minute, is neither more nor less than that which attends the comprehension of the rhythm of those muscles which act at longer intervals, as *e.g.* the diaphragm, the eyelids, or, during gastric digestion, the stomach.

From what has been said, it will be noticed that there is no exception to the rule, that, in the case of nerve and muscle, rest must alternate with work. We are apt to speak of the heart constantly acting, and to forget that it would be equally true to say that it is constantly resting. The difference from other muscles is only that the alternations of work and rest occur at shorter intervals.

The comparatively long-continued maintenance of the power of contracting in the case of the heart of a cold-blooded animal, introduces, moreover, no fresh difficulty in the comprehension of the subject. It is but an example of the rule that tissues which live and act at a slow rate, die at a slow rate also.

Although, under ordinary conditions, the apparatus of ganglia and nerve-fibres in the substance of the heart forms the medium through which its action is excited and rhythmically maintained, yet they, and, through them, the heart's contractions are regulated by nerves which pass to them from the higher nerve-centres. These nerves are branches from the pneumogastric and sympathetic.

The pneumogastric nerves are the media of an *inhibitory* or restraining influence over the action of the heart which is conveyed through them from the medulla oblongata, and which is always in operation. For, on dividing these nerves, the pulsations of the heart are increased in frequency; while an opposite effect is produced by stimulating them,—the transmission of a galvanic current of even moderate strength diminishing the number of pulsations or stopping the action of the heart altogether (in *diastole*).

This inhibitory influence may originate in the medulla oblongata, or may be merely *reflected* by it. As an example of the latter, the well-known effect on the heart of a violent blow on the epigastrium may be referred to. The stoppage of the heart's action is due to the conveyance of the stimulus by fibres of the sympathetic to the medulla oblongata, and its subsequent *reflection* through the pneumogastric to the heart's ganglia.

Through certain fibres of the sympathetic, the heart receives an *accelerating* influence from the medulla oblongata. These *accelerating* nerve-fibres, issuing from the spinal cord in the neck, reach the inferior cervical ganglion, and pass thence to the cardiac plexus, and so to the heart. Their function is shown in the quickened pulsation which follows stimulation of the spinal cord, when the latter has been cut off from all connection with the

heart, excepting that which is formed by the accelerating filaments from the inferior cervical ganglion. Unlike the inhibitory fibres of the pneumogastric, of which they may be considered the antagonists, the accelerating fibres are not continuously in action.

The connection of the heart with other organs by means of the nervous system, and the influences to which it is subject through them, are shown in a striking manner by the phenomena of disease. The influence of mental shock in arresting or modifying the action of the heart, the slow pulsation which accompanies compression of the brain, the irregularities and palpitations caused by dyspepsia or hysteria, are as good evidence of the connection of the heart with other organs through the nervous system, as any results obtained by direct experiment.

Effects of the Heart's Action.

That the contractions of the heart supply alone a sufficient force for the circulation of the blood, is established by the results of several experiments, of which the following is one of the most conclusive: — Dr. Sharpey injected bullock's blood into the thoracic aorta of a dog recently killed, after tying the abdominal aorta above the renal arteries, and found that, with a force just equal to that by which the ventricle commonly impels the blood in the dog, the blood which he injected into the aorta passed in a free stream out of the trunk of the vena cava inferior. It thus traversed both the systemic and hepatic capillaries; and when the aorta was not tied above the renals, blood injected under the same pressure flowed freely through the vessels of the lower extremities. A pressure equal to that of one and a half or two inches of mercury was, in the same way, found sufficient to propel blood through the vessels of the lungs.

But although it is true that the heart's action alone is sufficient to ensure the circulation, yet there exist several other forces which are, as it were, supplementary to the action of the heart, and assist it in maintaining the circulation. The principal of these

supplemental forces have been already alluded to, and will now be more fully pointed out.

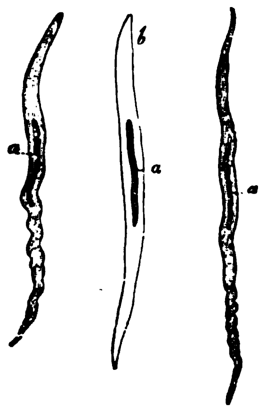
THE ARTERIES.

The walls of the arteries are composed of three principal coats, termed the *external* or *tunica adventitia*, the *middle*, and the *internal* coat or *tunica intima*, while the latter is lined within by a single layer of tessellated epithelium.

The external coat or tunica adventitia (figs. 91 and 92, *t. a.*), the strongest and toughest part of the wall of the artery, is formed of areolar tissue, with which is mingled throughout a network of elastic fibres. At the inner part of this outer coat the elastic network forms in most arteries so distinct a layer as to be sometimes called the *external elastic coat.*

The *middle coat* (fig. 92, *c. m.*) is composed of both muscular and elastic fibres, with a certain proportion of areolar tissue. In the larger arteries its thickness is comparatively as well as absolutely much greater than in the small, constituting, as it does, the greater part of the arterial wall.

Fig. 90.*

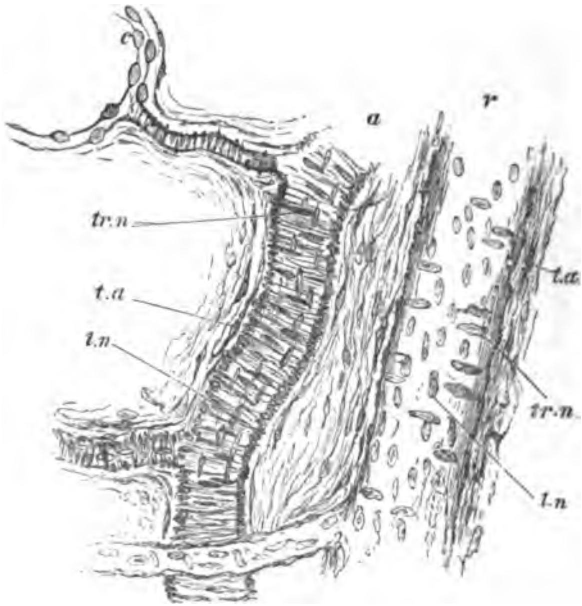


The muscular fibres, which are of the pale or unstriped variety (Fig. 90) (see Chapter on Motion), are arranged for the most part transversely to the long axis of the artery (fig. 91); while the elastic element, taking also a transverse direction, is disposed in the form of closely interwoven and branching fibres, which intersect in all parts the layers of muscular fibre. In arteries of various size there is a difference in the proportion of the muscular and elastic element, elastic tissue preponderating in the largest

* Fig. 90. Muscular fibre-cells from human arteries, magnified 350 diameters (Kölliker). *a*, nucleus; *b*, a fibre-cell treated with acetic acid.

arteries, while this condition is reversed in those of medium and small size.

Fig. 91.*



The *internal* arterial coat is formed by layers of elastic tissue, consisting in part of coarse longitudinal branching fibres, and in part of a very thin and brittle membrane which possesses little elasticity, and is thrown into folds or wrinkles when the artery contracts. This latter membrane, the striated or fenestrated coat of Henle (fig. 94), is peculiar in its tendency to curl up, when peeled off from the artery, and in the perforated and streaked appearance which it presents under the microscope. Its inner

* Fig. 91. Blood-vessels from mesocolon of rabbit. *a. Artery*, with two branches, showing *tr. n.* nuclei of transverse muscular fibres; *l. n.* nuclei of endothelial lining; *t. a.* tunica adventitia. *v. Vein.* Here the transverse nuclei are more oval than those of the artery. The vein receives a small branch at the lower end of the drawing; it is distinguished from the artery among other things by its straighter course and larger calibre. c. Capillary, showing nuclei of endothelial cells. × 300. (Schofield).

surface is lined with a delicate layer of epithelium, composed of thin squamous elongated cells (fig. 93, *a.*), which make it smooth and polished, and furnish a nearly impermeable surface, along which the blood may flow with the smallest possible amount of resistance from friction.

Fig. 92.*

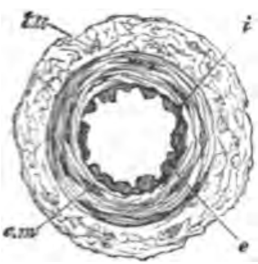
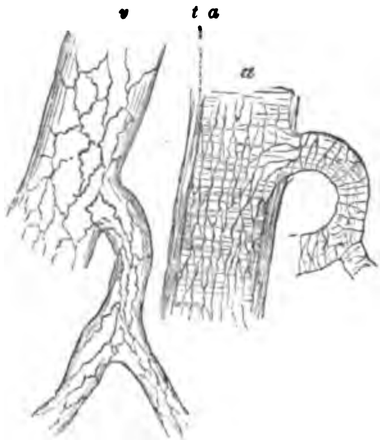


Fig. 93.†



Immediately external to the epithelial lining of the artery is a fine connective tissue, sub-epithelial layer, with branched corpuscles. Thus the internal coat consists of three parts, (*a*) an epithelial lining, (*b*) the sub-epithelial layer just mentioned, (*c*) elastic layers.

The walls of the arteries, with the possible exception of the epithelial lining and the layers of the internal coat immediately

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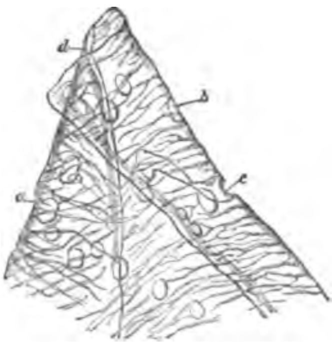
* Fig. 92. Transverse section of small artery from soft palate. *e*, endothelial lining, the nuclei of the cells are shown; *i*, elastic tissue of the intima, which is a good deal folded; *c. m.* circular muscular coat, showing nuclei of the muscle cells; *t. a.* tunica adventitia. × 300. (Schofield).

† Fig. 93. Two blood-vessels from a frog's mesentery, injected with nitrate of silver, showing the outlines of the endothelial cells. *a. Artery.* The endothelial cells are long and narrow; the transverse markings indicate the muscular coat. *t. a.* Tunica adventitia. *v. Vein.* Showing the shorter and wider endothelial cells with which it is lined. *c, c.* Two capillaries entering the vein. (Schofield).

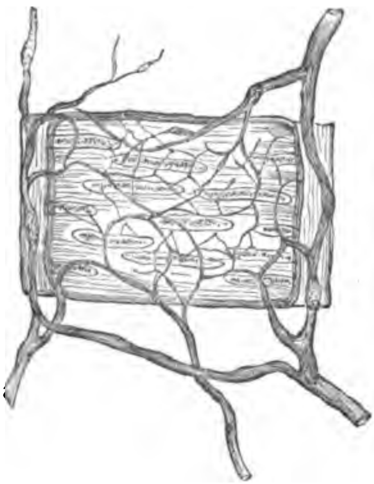
outside it, are not nourished by the blood which they convey, but are, like other parts of the body, supplied with little arteries, ending in capillaries and veins, which, branching throughout the external coat, extend for some distance into the middle, but do not reach the internal coat. These nutrient vessels are called *vasa vasorum*. Nerve-fibres are also supplied to the walls of the arteries.

Fig. 94.*



Most arteries are surrounded by a plexus of sympathetic nerves, which twine around the vessel very much like ivy round a tree; and ganglia are found at frequent intervals. The smallest arteries and capillaries are similarly surrounded by a very delicate network of non-medullated nerve-fibres, many of which appear to end in the nuclei of the transverse muscular fibres (fig. 95). It is doubtless through these plexuses that the calibre of the vessels is regulated by the nervous system (p. 188).

Fig. 95.†



The function of the arteries is to convey blood from the heart to all parts of the body, and each tissue which enters into the construction of an artery has a special purpose to serve in this distribution.

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* Fig. 94. Portion of fenestrated membrane from the femoral artery. × 200. *a*, *b*, *c*, perforations (Henle).

† Fig. 95. Ramification of nerves and termination in the muscular coat of a small artery of the frog. (Arnold).

(1.) The external coat forms a strong and tough investment, which, though capable of extension, appears principally designed to strengthen the arteries and to guard against their excessive distension from the force of the heart's action. It is this coat which alone prevents the complete severance of an artery when a ligature is tightly applied; the internal and middle coats being usually divided. In it, too, the little *vasa vasorum* (p. 172) find a suitable tissue in which to subdivide for the supply of the arterial coats.

(2.) The purpose of the elastic tissue, which enters so largely into the formation of all the coats of the arteries, is, (*a*). To guard the arteries from the suddenly exerted pressure to which they are subjected at each contraction of the ventricles. In every such contraction, the contents of the ventricles are forced into the arteries more quickly than they can be discharged into and through the capillaries. The blood therefore being, for an instant, resisted in its onward course, a part of the force with which it was impelled is directed against the sides of the arteries; under this force their elastic walls dilate, stretching enough to receive the blood, and as they stretch, becoming more tense and more resisting. Thus, by yielding, they, as it were, break the shock of the force impelling the blood.

On the subsidence of the pressure, when the ventricles cease contracting, the arteries are able, by the same elasticity, to resume their former calibre; and in thus doing, they manifest (*b*) another chief purpose of their elasticity, that, namely, of equalizing the current of the blood by maintaining pressure on the blood in the arteries during the periods at which the ventricles are at rest or dilating. If some such method as this had not been adopted—if for example the arteries had been rigid tubes, the blood, instead of flowing as it does, in a constant stream, would have been propelled through the arterial system in a series of jerks corresponding to the ventricular contractions, with intervals of almost complete rest during the inaction of the ventricles. But in the actual condition of the arteries, the force of the successive contractions of the ventricles is expended partly in the direct propulsion of the blood, and partly in the

dilatation of the elastic arteries; and in the intervals between the contractions of the ventricles, the force of the recoiling and contracting arteries is employed in continuing the same direct propulsion. Of course, the pressure exercised by the recoiling arteries is equally diffused in every direction through the blood, and the blood would tend to move backwards as well as onwards, but all movement backwards is prevented by the closure of the semi-lunar arterial valves (p. 151), which takes place at the very commencement of the recoil of the arterial walls.

By this exercise of the elasticity of the arteries, all the force of the ventricles is made advantageous to the circulation; for that part of their force which is expended in dilating the arteries, is restored in full when they recoil. There is thus no loss of force; but neither is there any gain, for the elastic walls of the artery cannot originate any force for the propulsion of the blood—they only restore that which they received from the ventricles. The force with which the arteries are dilated every time the ventricles contract, might be said to be received by them in store, to be all given out again in the next succeeding period of dilatation of the ventricles. It is by this equalizing influence of the successive branches of every artery that, at length, the intermittent accelerations produced in the arterial current by the action of the heart, cease to be observable, and the jetting stream is converted into the continuous and equable movement of the blood which we see in the capillaries and veins.

In the production of a continuous stream of blood in the smaller arteries and capillaries, the resistance which is offered to the blood-stream in the capillaries (p. 196), is a necessary agent. Were there no greater obstacle to the *escape* of blood from the arteries than exists to its *entrance* into them from the heart, the stream would be intermittent, notwithstanding the elasticity of the walls of the arteries.

(*c*.) By means of the elastic tissue in their walls (and of the muscular tissue also), the arteries are enabled to dilate and contract readily in correspondence with any temporary increase or diminution of the total quantity of blood in the body; and

within a certain range of diminution of the quantity, still to exercise due pressure on their contents.

The elastic coat, however, not only assists in restoring the normal calibre of an artery after temporary *dilatation*, but also, (*d*.) may assist in restoring it after *diminution* of the calibre, whether this be caused by a temporary contraction of the muscular coat, or the application of a compressing force from without. This action of the elastic tissue in arteries, is well shown in arteries which contract after death, but regain their average patency on the cessation of post-mortem rigidity (p. 177). (*e*.) By means of their elastic coat the arteries are enabled to adapt themselves to the different movements of the several parts of the body.

With regard to the purpose served by the *muscular coat* of the arteries, there appears no sufficient reason for supposing that it assists, to more than a very small degree, in propelling the onward current of blood. That it contributes, however, in some degree, to the forces concerned in the circulation of the blood, may be fairly inferred not only from the presence of muscular fibres, but from the actual observations of contractions of the arteries during life, in some of the lower animals, (rabbit, bat, frog,) the rhythm of which is quite different from that of the heart. (Wharton Jones, Schiff, Ludwig, Brunton.)

The most important office of the muscular coat, is (2) that of regulating the quantity of blood to be received by each part, and of adjusting it to the requirements of each, according to various circumstances, but, chiefly, according to the activity with which the functions of each are at different times performed. The amount of work done by each organ of the body varies at different times, and the variations often quickly succeed each other, so that, as in the brain for example, during sleep and waking, within the same hour a part may be now very active and then inactive. In all its active exercise of function, such a part requires a larger supply of blood than is sufficient for it during the times when it is comparatively inactive. It is evident that the heart cannot regulate the supply to each part at different periods; neither could this be regulated by any general and uni-

form contraction of the arteries; but it may be regulated by the power which the arteries of each part have, in their muscular tissue, of contracting so as to diminish, and of passively dilating or yielding so as to permit an increase of, the supply of blood, according to the requirements of the part to which they are distributed. And thus, while the ventricles of the heart determine the total quantity of blood, to be sent onwards at each contraction, and the force of its propulsion, and while the large and merely elastic arteries distribute it and equalise its stream, the smaller arteries, in addition, regulate and determine, by means of their muscular tissue, the proportion of the whole quantity of blood which shall be distributed to each part.

It must be remembered, however, that this regulating function of the arteries is itself governed and directed by the nervous system (p. 188).

Another function of the muscular element of the middle coat of arteries is, doubtless (3), to co-operate with the elastic in adapting the calibre of the vessels to the quantity of blood which they contain. For the amount of fluid in the blood-vessels varies very considerably even from hour to hour, and can never be quite constant; and were the elastic tissue only present, the pressure exercised by the walls of the containing vessels on the contained blood would be sometimes very small, and sometimes inordinately great. The presence of a muscular element, however, provides for a certain uniformity in the amount of pressure exercised; and it is by this adaptive, uniform, gentle, muscular contraction, that the *tone* of the blood-vessels is maintained. Deficiency of this *tone* is the cause of the soft and yielding pulse, and its unnatural excess, of the hard and tense one.

The elastic and muscular contraction of an artery may also be regarded as fulfilling a natural purpose when (4), the artery being cut, it first limits and then, in conjunction with the coagulated fibrin, arrests the escape of blood. It is only in consequence of such contraction and coagulation that we are free from danger through even very slight wounds; for it is only when the artery is closed that the processes for the more permanent and secure prevention of bleeding are established.

(1.) When a small artery in the living subject is exposed to the air or cold, it gradually but manifestly contracts. Hunter observed that the posterior tibial artery of a dog when laid bare, became in a short time so much contracted as almost to prevent the transmission of blood; and the observation has been often and variously confirmed. Simple elasticity could not effect this; for after death, when the vital muscular power has ceased, and the mechanical elastic one alone operates, the contracted artery dilates again.

(2.) When an artery is cut across, its divided ends contract, and the orifices may be completely closed. The rapidity and completeness of this contraction vary in different animals; they are generally greater in young than in old animals; and less, apparently, in man than in animals. In part this contraction is due to elasticity, but in part, no doubt, to muscular action; for it is generally increased by the application of cold, or of any simple stimulating substances, or by mechanically irritating the cut ends of the artery, as by picking or twisting them. Such irritation would not be followed by these effects, if the arteries had no other power of contracting than that depending upon elasticity.

(3.) The contractile property of arteries continues many hours after death, and thus affords an opportunity of distinguishing it from elasticity. When a portion of an artery, the splenic, for example, of a recently killed animal, is exposed, it gradually contracts, and its canal may be thus completely closed: in this contracted state it remains for a time, varying from a few hours to two days: then it dilates again, and permanently retains the same size. If, while contracted, the artery be forcibly distended, its contractility is destroyed, and it holds a middle or natural size.

This persistence of the contractile property after death was well shown in an observation of Hunter, which may be mentioned as proving, also, the greater degree of contractility possessed by the smaller than by the larger arteries. Having injected the uterus of a cow, which had been removed from the animal upwards of twenty-four hours, he found, after the lapse of another day, that the larger vessels had become much more turgid than when he injected them, and that the smaller arteries had contracted so as to force the injection back into the larger ones.

The results of an experiment which Hunter made with the vessels of an umbilical cord prove still more strikingly the long continuance of the contractile power of arteries after death. In a woman delivered on a Thursday afternoon, the umbilical cord was separated from the fœtus, having been first tied in two places, and then cut between, so that the blood contained in the cord and placenta was confined in them. On the following morning, Hunter tied a string round the cord, about an inch below the other ligature, that the blood might still be confined in the placenta and remaining cord. Having cut off this piece, and allowed all the blood to escape from its vessels, he attentively observed to what size the ends of the cut arteries were brought by the elasticity of their coats, and then laid aside the piece of cord to see the influence of the contractile power of its vessels. On Saturday morning, the day after, the mouths of the arteries were completely closed up. He repeated the experiment the same day with another portion of the same cord, and on the following morning found the results to be precisely similar. On the Sunday, he performed the experiment the third

time, but the artery then seemed to have lost its contractility, for on the Monday morning, the mouths of the cut arteries were found open. In each of these experiments there was but little alteration perceived in the orifices of the veins.

(4.) The influence of cold in increasing the contraction of a divided artery has been referred to: it has been shown, also, by Schwann, in an experiment on the mesentery of a living toad. Having extended the mesentery under the microscope, he placed upon it a few drops of water, the temperature of which was some degrees lower than that of the atmosphere. The contraction of the vessels soon commenced, and gradually increased until, at the expiration of ten or fifteen minutes, the diameter of the canal of an artery, which at first was 0·0724 of an English line, was reduced to 0·0276. The arteries then dilated again, and at the expiration of half an hour had acquired nearly their original size. By renewing the application of the water, the contraction was reproduced: in this way the experiment could be performed several times on the same artery. It is thus proved, that cold will excite contraction in the walls of very small, as well as of comparatively large arteries: it could not produce such contraction in a merely elastic substance; but it is a stimulus to the organic muscular fibres in many other parts, as well as in the arterial coat; as, *e.g.*, in the skin, the dartos, and the walls of the bronchi.

(5.) Evidence of the muscular contractility of the arterial coats is furnished by the experiments of Ed. and E. H. Weber, and of Professor Kölliker, in which they applied the stimulus of electro-magnetism to small arteries. The experiments of the Webers were performed on the small mesenteric arteries of frogs; and the most striking results were obtained when the diameter of the vessels examined did not exceed from $\frac{1}{3}$ to $\frac{1}{12}$ of a Paris line. When a vessel of this size was exposed to the electric current, its diameter in from five to ten seconds, became one-third less, and the area of its section about one-half. On continuing the stimulus, the narrowing gradually increased, until the calibre of the tube became from three to six times smaller than it was at first, so that only a single row of blood-corpuscles could pass along it at once; and eventually the vessel was closed and the current of blood arrested.

Mr. Savory has shown that the natural state of all arteries, in regard at least to their length, is one of tension—that they are always more or less stretched, and ever ready to recoil by virtue of their elasticity, whenever the opposing force is removed. The extent to which the divided extremities of arteries retract is a measure of this tension, not of their elasticity.

The Pulse.

The jetting movement of the blood, due to the intermittent action of the heart, which the elasticity of the arteries converts

into an uniform motion, in the arterioles (smallest arteries) and capillaries, is the cause of *the pulse*. As the blood is not able to pass through the arteries so quickly as it is forced into them by the ventricle, on account of the resistance it experiences in the small arteries and capillaries, a part of the force with which the heart impels the blood is exercised upon the walls of the vessels which it distends—thus producing the arterial tension or blood-pressure, to be afterwards referred to (p. 184). The maximum of that tension, which follows each beat of the heart, is called the *pulse*. The distension of each artery increases both its length and its diameter. In their elongation, the arteries change their form, the straight ones becoming slightly curved, or having such a tendency, and those already curved becoming more so;* but they recover their previous form as well as their diameter when the ventricular contraction ceases, and their elastic walls recoil. The increase of their curves which accompanies the distension of arteries, and the succeeding recoil, may be well seen in the prominent temporal artery of an old person. The elongation of the artery is in such a case quite manifest. The mind cannot distinguish the sensation produced by the dilatation from that produced by the elongation and curving; that which it perceives most plainly, however, is the dilatation, or return, more or less, to the cylindrical form, of the artery which has been partially flattened by the finger.

The pulse—due to any given beat of the heart—is not perceptible at the same moment in all the arteries of the body. Thus,—it can be felt in the carotid a very short time before it is perceptible in the radial artery, and in this vessel again before the dorsal artery of the foot. The delay in the beat is in proportion to the distance of the artery from the heart, but the difference in time between the beat of any two arteries never exceeds probably $\frac{1}{6}$ to $\frac{1}{8}$ of a second.

* There is, perhaps, an exception to this in the case of the aorta, of which the curve is by some supposed to be diminished when it is elongated; but if this be so, it is because only one end of the arch is immoveable; the other end, with the heart, may move forward slightly when the ventricles contract.

It was formerly supposed that the pulse was caused, not by the direct action of the ventricle, but by the propagation of a wave in consequence of the elastic recoil of the large arteries, after their distension; and successive acts of dilatation and recoil, extending along the arteries in the direction of the circulation, were supposed to account for the later appearance of the pulse in the vessels most distant from the heart. The fact, however, that the pulse is perceptible in every part of the arterial system previous to the occurrence of the second sound of the heart, that is, previous to the closure of the aortic valves, is a fatal objection to this theory. For, if the pulse were the effect of a wave propagated by the alternate dilatation and contraction of successive portions of the arterial tube, it ought, in all the arteries except those nearest to the heart, to follow or coincide with, but could never precede, the second sound of the heart; for the first effect of the elastic recoil of the arteries first dilated is the closure of the aortic valves; and their closure produces the second sound.

The theory which seems to reconcile all the facts of the case, and especially those two which appear most opposed, namely, that the pulse always precedes the second sound of the heart, and yet is later in the arteries far from the heart than in those near it, may be thus stated:—It supposes that the blood which is impelled onwards by the left ventricle does not so impart its pressure to that which the arteries already contain, as to dilate the whole arterial system at once; but that it enters the arteries, it displaces and propels that which they before contained, and flows on with what may be called a *head-wave*, like that which is formed when a rapid stream of water overtakes another moving more slowly. The slower stream offers resistance to the more rapid one, till their velocities are equalized: and, because of such resistance, some of the force of the more rapid stream of blood just expelled from the ventricle, is diverted laterally, and with the rising of the wave the arteries nearest the heart are dilated and elongated. They do not at once recoil, but continue to be distended so long as blood is entering them from the ventricle. The wave at the head of the more rapid stream of blood runs on, propelled and maintained in its velocity by the continuous contraction of the ventricle: and it thus dilates in succession every portion of the arterial system, and produces the pulse in all. At length, the whole arterial system (wherein a pulse can be felt) is dilated; and at this time when the wave we have supposed has reached all the smaller arteries, the entire system may be said to be simultaneously dilated; then it begins to contract, and the contractions of its several parts ensue in the same succession as the dilatations, commencing at the heart. The contraction of the first portion produces the closure of the valves and the second sound of the heart; and both it and the progressive contractions of all the more distant parts maintain, as already said, that pressure on the blood during the inaction of the ventricle, by which the stream of the arterial blood is sustained between the jets, and is finally equalized by the time it reaches the capillaries.

It may seem an objection to this theory, that it would probably require a larger quantity of blood to dilate all the arteries that can be discharged by the ventricle at each contraction. But the quantity necessary for such a purpose is less than might be supposed. Injections of the arteries prove that, including all down to those of about one-eighth of a line in diameter,

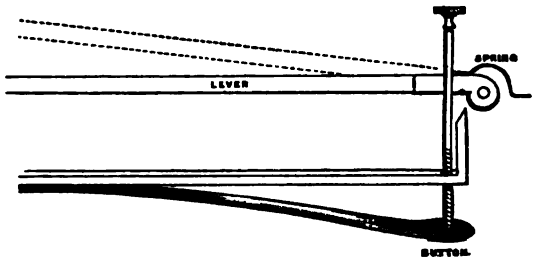
they do not contain on an average more than one and a half pints of fluid, even when distended. There can be no doubt, therefore, that the three or four ounces which the ventricle discharges at each contraction, being added to that which already fills the arteries, is sufficient to distend them all.

A distinction must be carefully made between the passage of the *wave* along the arteries, and the velocity of the *stream* (p. 207) of blood. Both wave and current are present; but the rates at which they travel are very different; that of the wave, 28·5 feet per second (E. H. Weber), being twenty or thirty times as great as that of the current.

The Sphygmograph.

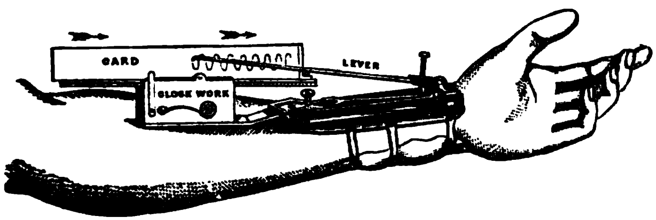
A great deal of light has been thrown on what may be called the form of the pulse by the sphygmograph (figs. 96 and 97).

Fig. 96.*



The principle on which the sphygmograph acts is very simple (see fig. 96). The small button replaces the finger in the act of

Fig. 97.*



taking the pulse, and is made to rest lightly on the artery, the pulsations of which it is desired to investigate. The up-and-

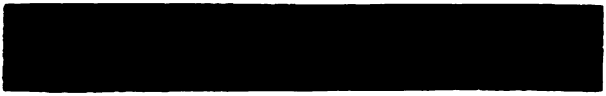
* Fig. 96. Diagram of the mode of action of the Sphygmograph.
† Fig. 97. The Sphygmograph applied to the arm.

down movement of the button is communicated to the lever, to the hinder end of which is attached a slight spring, which allows the lever to move up, at the same time that it is just strong enough to resist its making any sudden jerk, and in the interval of the beats also to assist in bringing it back to its original position. For ordinary purposes, the instrument is bound on the wrist (fig. 97).

It is evident that the beating of the pulse with the reaction of the spring will cause an up-and-down movement of the lever, and if the extremity of the latter be inked, it will write the effect on the card, which is made to move by clockwork in the direction of the arrow. Thus a tracing of the pulse is obtained, and in this way much more delicate effects can be seen, than can be felt on the application of the finger.

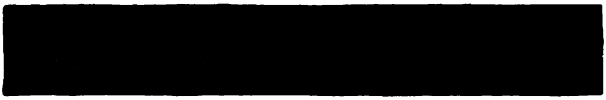
Fig. 98 represents a healthy pulse-tracing of the radial artery, but somewhat deficient in *tone*. On examination, we see that

Fig. 98.*



the up-stroke which represents the beat of the pulse is a nearly vertical line, while the down-stroke is very slanting, and interrupted by a slight re-ascent. The more vigorous the pulse, if it be healthy, the less is this re-ascent, and *vice versâ*. Fig. 99

Fig. 99.†



represents the tracing of a healthy pulse in which the tone of the vessel is better than in the last instance, and the down-stroke is therefore less interrupted.

In the large arteries, when at least there is much loss of *tone*, the up-stroke is double, the almost instantaneous pro-

* Fig. 98. Pulse-tracing of radial artery, somewhat deficient in *tone*.

† Fig. 99. Firm and long pulse of vigorous health.

pagation of the force of contraction of the left ventricle along the column of blood in the arteries, or the *percussion-impulse*

Fig. 100.*

as it is termed by Dr. Burdon-Sanderson, being sufficiently strong to jerk up the lever for an instant, while the *wave* of blood, rather more slowly propagated from the ventricle, catches it, so to speak, as it begins to fall, and again slightly raises it.

In the radial artery tracings, on the other hand, we see that the up-stroke is single. In this case the percussion-impulse is not sufficiently strong to jerk up the lever and produce an effect distinct from that of the systolic *wave* which immediately follows it, and which continues and completes the distension. In cases of feeble arterial tension, however, the percussion-impulse may be traced by the sphygmograph, not only in the carotid pulse, but to a less extent in the radial also (fig. 100).

In looking now at the down-stroke (fig. 98) in the tracings, we see that in the case of an artery with deficient *tone*, it is interrupted by a well-marked notch, or, in other words, that the descent is interrupted by a slight uprising. There are indications also of slighter irregularities or vibrations during the fall of the lever; while these alone are to be seen in the pulse of health, or, in other words, when the walls of the artery are of good tone (fig. 99). In some cases of disease the re-ascent is so considerable as to be perceptible to the finger, and this double beat has received the technical name of "dicrotous" pulse. As a diseased condition this has long been recognised, but it is only since the invention of the sphygmograph that it has been found to belong in a certain degree to the normal pulse also.

Various theories have been framed to account for the dicrotism

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* Fig. 100. Pulse-tracing of radial artery, with double apex.

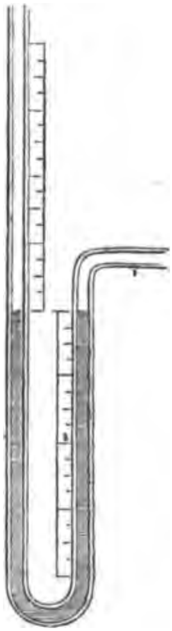
The above tracings are taken from Dr. Sanderson's work, "On the Sphygmograph."

of the pulse. By some, it is supposed to be due to the aortic valves, the sudden closure of which stops the incipient regurgitation of blood into the ventricle, and causes a momentary rebound throughout the arterial system; while Dr. Burdon-Sanderson considers it to be caused by a rebound from the periphery rather than from the central part of the circulating apparatus.

Pressure of the blood in the Arteries, or Arterial Tension.

From what has been previously said, it will have become evident that the blood in the arteries is always the subject of a certain amount of pressure, both during the action of the ventricle and in the intervals. In the former case this is the direct result of the force exercised by the contracting ventricle, and, in the latter, by the force with which the walls of the arteries recoil after distension; another necessary condition being the comparative difficulty with which the blood escapes into the veins through the arterioles and capillaries (p. 179).

Fig. 101.

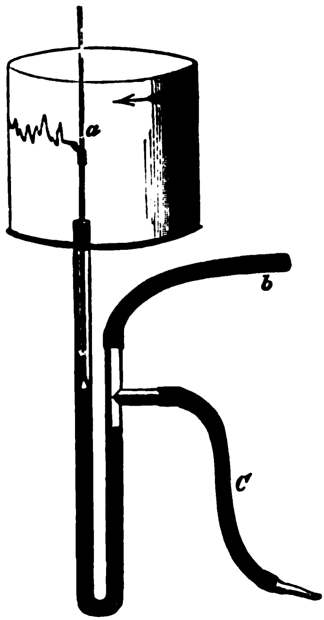


The instrument employed for the purpose of gauging the amount of the blood-pressure or arterial tension is a mercurial manometer (fig. 101), of which the short horizontal limb (1) is connected, by means of an elastic tube and canula, with the interior of an artery; a solution of sodium or potassium carbonate being previously introduced into this part of the apparatus to prevent coagulation of the blood. The blood-pressure is thus communicated to the upper part of the mercurial column (2); and the depth to which the latter sinks, added to the height to which it rises in the other (3), will give the height of the mercurial column which the blood-pressure balances; the weight of the soda solution being subtracted.

For the estimation of the arterial tension at any given moment, no further apparatus than this, which is called Poiseuille's *hæmadynamometer*, is necessary; but for noting the *variations* of pressure in the arterial system, as well as its absolute amount, the instrument is usually combined with a *registering* apparatus and in this form is called a *kymograph*.

The kymograph, invented by Ludwig, is composed of a hæmadynamometer, the open mercurial column of which supports a floating piston and

Fig. 102.*



vertical rod, with short horizontal pen (fig. 102). The pen is adjusted in contact with a sheet of paper, which is caused to move at an uniform rate

Fig. 103.†

by clockwork; and thus the up-and-down movements of the mercurial column, which are communicated to the rod and pen, are marked or

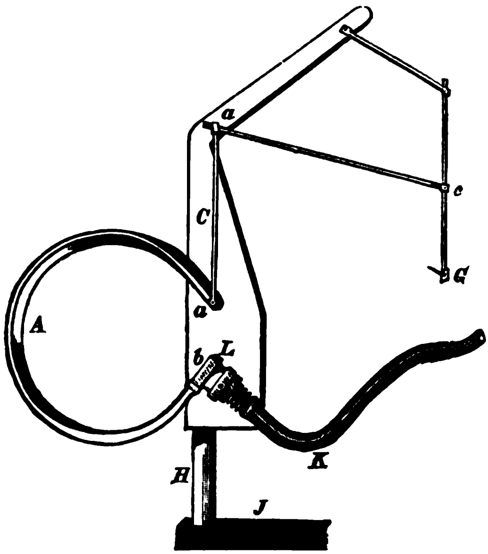
* Fig. 102. Diagram of Mercurial Kymograph. *a*, Floating rod and pen. The arrow is placed on the revolving paper cylinder, on which are inscribed the movements of the pen in contact with it. *b*, tube, which communicates with a bottle containing an alkaline solution. *c*, elastic tube and canula, the latter being intended for insertion in an artery.

† Fig. 103. Normal tracing of arterial pressure obtained with the mercurial kymograph in the rabbit. (Burdon-Sanderson).

registered on the moving paper, as in the registering apparatus of the sphygmograph, and minute variations are graphically recorded (fig. 103).

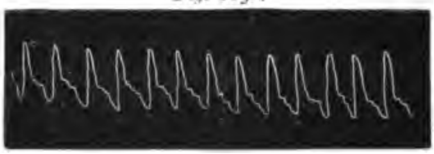
For some purposes the *spring-kymograph* of Professor Fick (fig. 104) is pre-

Fig. 104.*



ferable to the mercurial kymograph. It consists of a hollow C-shaped spring, filled with fluid, the interior of which is brought into connection with the

Fig. 105.†



interior of an artery, by means of an elastic tube and canula, as in the last case (fig. 102, *C.*). In response to the pressure transmitted to its interior, the

* Fig. 104. Fick's Spring Kymograph. A. Hollow C-spring, fixed at one end, *b*, to a piece of board, L, which is connected by an upright, H, to the wooden support, J. The other end *a*, is freely moveable, and its movements are communicated by the rod, C, to the lever, *a e*, and thus to the writing needle, G. The C-spring is filled with alcohol, and its interior communicates with the artery through the tube K, which is filled with a soda-solution, and to which is attached an elastic tube and canula.

† Fig. 105. Normal arterial tracing obtained with Fick's kymograph in the dog. (Burdon-Sanderson).

spring tends to straighten itself, and the movement thus produced is communicated by means of a lever to a writing-needle, and registering apparatus.

Fig. 105 exhibits an ordinary arterial pulse-tracing, as obtained by the spring-kymograph.

Poiseuille calculated, from the mean result of several observations on horses and dogs, that the blood-pressure in any large artery is capable of supporting a mercurial column of rather more than six inches in height; and that to measure the absolute amount of this pressure in any artery, it is necessary merely to multiply the area of its transverse section by the height of the column of mercury which is already known to be supported by the blood-pressure in any part of the arterial system. The weight of a column of mercury thus found will represent the pressure of the blood. Calculated in this way, he supposed that the blood-pressure in the human aorta is equal to 4 lb. 4 oz. avoirdupois; that in the aorta of the horse being 11 lb. 9 oz.; and that in the radial artery at the human wrists only 4 drs. Supposing the muscular power of the right ventricle to be only one-half that of the left, the blood-pressure in the pulmonary artery will be only 2 lb. 2 oz. avoirdupois.

The amounts above stated represent the arterial tension at the time of the ventricular contraction.

Many circumstances cause considerable variations in the amount of the blood-pressure. The following are the chief:—

1. The alternating systole and diastole of the heart; the arterial tension increasing during systole and diminishing during diastole. The greater the frequency, moreover, of the heart's contractions, the greater is the blood-pressure, *cæteris paribus;* although this effect is not constant, as it may be compensated for by the delivery into the arteries at each beat of a comparatively small quantity of blood. The greater the quantity of blood expelled from the heart at each contraction the greater is the blood-pressure.

2. The respiratory movements. Arterial tension is increased during inspiration, and falls during expiration. (Burdon-Sanderson.)

3. Variations in the degree of contraction of the smaller arteries modify the blood-pressure by favouring or impeding the accumulation of blood in the arterial system which follows every contraction of the heart (p. 179); the contraction of the arterial walls increasing the blood-pressure, while their relaxation lowers it.

4. The greater the total quantity of blood, the greater, *cæteris paribus,* is the blood-pressure.

Acting indirectly, that is, by influencing one or more of the above mentioned conditions which act directly, the nervous system powerfully affects in various ways the blood-pressure. (See Sections on the Influence of the Nervous System on the Heart and Bloodvessels.)

A due amount of blood-pressure is, in the higher animals, one of the conditions of life; inasmuch as it is only under such circumstances that the blood is supplied to the various organs and tissues with constancy and force sufficient for the maintenance of their functions. This is best shown by the effect of its absence on the higher organs of the nervous system; lessening of the blood-pressure below a certain amount being invariably accompanied by a temporary or permanent cessation of their functions. Thus, *syncope* or fainting is caused by diminished blood-pressure in the cerebral arteries, depending either upon feebleness of the heart's action, or upon some other cause which diminishes the arterial tension, as hæmorrhage or the like.

Influence of the Nervous System on the Arteries.

The arteries of all parts of the body are supplied with nerve-fibres by the sympathetic system. Thus, the blood-vessels of the head and neck receive fibres from the superior cervical ganglion, those of the thorax from the cervical and upper dorsal prævertebral ganglia, and so forth; the fibres, however, being frequently bound up in cerebro-spinal nerve bundles, and distributed as offsets from them.

The *tone* of the arteries, or, in other words, the amount of contraction of the muscular fibres of the arterial coats (p. 176), which is ever varying, depends entirely on the influence which is exercised through these *vasomotor* branches of the sympathetic. If one of them be stimulated—as, for example, by applying an electric current, the arteries to which its branches are distributed contract, and diminish the stream of blood which is flowing through them. If, on the other hand, the nerve be divided, the arteries are paralysed, that is, they lose their muscular tone altogether, and become dilated. (Brown-Séquard.)

The most usual experiment in illustration of these facts is performed by

exposing in a rabbit the cervical sympathetic and dividing it. The blood-vessels of the corresponding side of the head and neck, thus paralysed, and unable to contract on the stream of blood in their interior, become dilated. The effect is best seen in the ear, the blood-vessels of which become manifestly larger than those of the opposite side; while the part becomes both redder and warmer from the increased quantity of blood which circulates in it. On galvanizing the distal cut end of the nerve, the muscular fibres of the blood vessels are caused to contract again; and while the stimulus lasts, the ear and other parts become paler, colder, and less sensitive than natural.

A familiar example of similar physiological conditions, arising from a different cause, is the act of blushing which is produced by a temporary paralysis of blood-vessels, and consequently enlarged stream of blood.

Experiments by Ludwig and others show that the vasomotor nerves come primarily from grey matter (vasomotor centre) in the interior of the medulla oblongata, between the *calamus scriptorius* and the *corpora quadrigemina*. Thence the vasomotor fibres pass down in the interior of the spinal cord, and issuing with the anterior roots of the spinal nerves, traverse the various ganglia on the præ-vertebral cord of the sympathetic, and, accompanied by branches from these ganglia, pass to their destination. By the vasomotor nerve-centre in the medulla, which is always in action, more or less, the *tone* of all the blood-vessels is regulated; but secondary or subordinate centres probably exist in the ganglia of various regions of the body, and through these, directly, under ordinary circumstances, vasomotor changes are also effected.

The nerve-impulses which issue from the vasomotor nerve-centres are for the most part the results of reflex action, and may lead to either contraction or dilatation of the blood-vessels. Thus,—on stimulating the sensory nerve of a part, the stimulus, if sufficiently strong, leads to contraction of all the blood-vessels of the body, except those which are situate in the region to which the sensory nerve in question is distributed; and here the blood-vessels become dilated. In the former case (contraction) the action is called *excito-motor*, and in the latter *inhibitory*. A familiar example of such inhibitory action is afforded by the redness of the skin, which follows scratching or other slight injury.

Cyon and Ludwig discovered that a remarkable power is

exercised on the dilatation of the blood-vessels by a small nerve which arises, in the rabbit, from the superior laryngeal branch, or from this and the trunk of the pneumogastric nerve, and after communicating with filaments of the inferior cervical ganglion proceeds to the heart. If this nerve be divided, and its upper extremity feebly galvanised, an inhibitory influence is conveyed to the vasomotor centre in the medulla oblongata, so as to cause, by reflex action, dilatation of the principal blood-vessels, with diminution of the force and frequency of the heart's action. From the remarkable lowering of the blood pressure thus produced, this branch of the vagus is called the *depressor* nerve; and it is presumed to be a means of conveying to the vasomotor centre indications of such conditions of the heart as require a diminution of the tension in the blood-vessels; as, for example, when the heart cannot, with sufficient ease, propel blood into the already too full or too tense arteries.

The influence of vasomotor changes in one part or region in relation to other parts of the body, is most notably shown by experiments on the function of the splanchnic nerves. These nerves contain the greater part of the vasomotor fibres of the blood-vessels of the abdominal viscera; and, as the blood supply of the latter is normally very large, variations in its quantity will largely affect the blood pressure of all parts. On stimulating the splanchnics and thus causing contraction of the abdominal vessels, the general blood-pressure rises very considerably. On dividing these nerves, on the other hand, the abdominal blood-vessels dilate, and the blood-pressure falls; and so large and numerous are the vessels of the abdominal viscera that, when fully dilated in consequence of the division of their nerves, they contain a great part of the whole mass of blood, and as a consequence other parts are drained of their due proportion. The effect of such a condition of the abdominal system of blood-vessels on other parts has, indeed, been compared to that of a large internal hæmorrhage; and the symptoms produced in a living animal by division of the splanchnics, prove the justice of the comparison.

THE CAPILLARIES.

In all organic textures, exept some parts of the corpora cavernosa of the penis, and of the uterine placenta, and of the spleen, the transmission of the blood from the minute branches of the arteries to the minute veins is effected through a network of microscopic vessels, called *capillaries*. These may be seen in all minutely injected preparations; and during life, by the aid

of the microscope, in any transparent vascular parts,—such as the web of the frog's foot, the tail or external branchiæ of the tadpole, or the wing of the bat.

The branches of the minute arteries form repeated anastomoses with each other and give off the capillaries which, by their anastomoses, compose a continuous and uniform network, from which the venous radicles, on the other hand, take their rise (fig. 106). The reticulated vessels connecting the arteries and veins are called *capillary*, on account of their minute size; and *intermediate* vessels, on account of their position. The point at which the arteries terminate and the minute veins commence, cannot be exactly defined, for the transition is gradual; but the capillary network has, nevertheless, this peculiarity, that the small vessels which compose it maintain the same diameter throughout; they do not diminish in diameter in one direction, like arteries and veins; and the meshes of the network that they compose are more uniform in shape and size than those formed by the anastomoses of the minute arteries and veins.

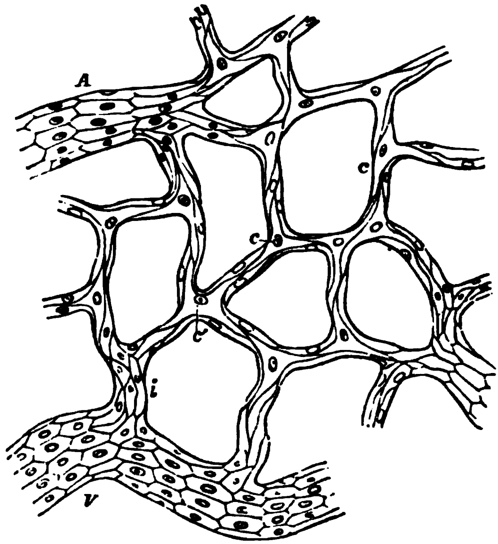
Fig. 106.*

The structure of the capillaries is much more simple than that of the arteries or veins. Their walls are composed of a single layer of elongated or radiate, flattened and nucleated cells, so joined and dovetailed together as to form a continuous transparent membrane (fig. 107). Outside these cells, in the larger capillaries, there is a structureless, or very finely fibrillated membrane, on the inner surface of which they are laid down.

* Fig. 106. Blood-vessels of an intestinal villus, representing the arrangement of capillaries between the ultimate venous and arterial branches; *a, a,* the arteries; *b,* the vein.

In some cases this membrane is nucleated, and may then be regarded as a miniature representative of the *tunica adventitia* of arteries.

Fig. 107.*



Here and there at the junction of two or more of the delicate endothelial cells which compose the capillary wall, *stomata* may be seen resembling those in serous membranes (p. 63). The endothelial cells are often continuous at various points with processes of adjacent connective tissue corpuscles. (An explanation of this latter appearance will be found in the Chapter on Development.)

Capillaries are surrounded by a delicate nerve-plexus resembling, in miniature, that of the larger blood-vessels.

The *diameter* of the capillary vessels varies somewhat in the

* Fig. 107. Magnified view of capillary vessels from the bladder of the cat. —A, V, an artery and a vein; *i*, transitional vessel between them and *c*, *c*, the capillaries. The muscular coat of the larger vessels is left out in the figure to allow the epithelium to be seen: at *c'*, a radiate epithelium scale with four pointed processes, running out upon the four adjoining capillaries (after Chrzonszczewsky, Virch. Arch. 1866).

different textures of the body, the most common size being about $\frac{1}{3000}$th of an inch. Among the smallest may be mentioned those of the brain, and of the follicles of the mucous membrane of the intestines; among the largest, those of the skin, and especially those of the medulla of bones.

The size of capillaries varies also in different animals in relation to the size of their blood-corpuscles: thus, in the Proteus, the capillary circulation can just be discerned with the naked eye.

The *form* of the capillary network presents considerable variety in the different textures of the body: the varieties consisting principally of modifications of two chief kinds of mesh, the rounded and the elongated. That kind in which the meshes or interspaces have a roundish form is the most common, and prevails in those parts in which the capillary network is most dense, such as the lungs (fig. 108), most glands, and mucous

Fig. 108.*

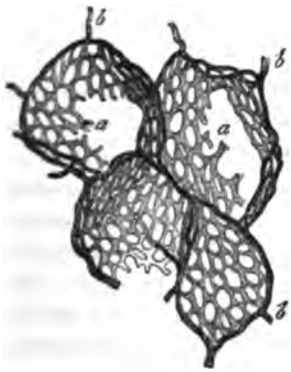


Fig. 109.†

membranes, and the cutis. The meshes of this kind of network are not quite circular, but more or less angular, sometimes presenting a nearly regular quadrangular or polygonal form,

* Fig. 108. Network of capillary vessels of the air-cells of the horse's lung, magnified. *a*, *a*, capillaries proceeding from *b*, *b*, terminal branches of the pulmonary artery (Frey).

† Fig. 109. Injected capillary vessels of muscle, seen with a low magnifying power (Sharpey).

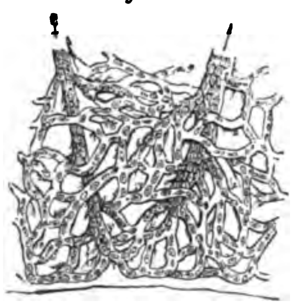
but being more frequently irregular. The capillary network with elongated meshes (fig. 109) is observed in parts in which the vessels are arranged among bundles of fine tubes or fibres, as in muscles and nerves. In such parts, the meshes usually have the form of a parallelogram, the short sides of which may be from three to eight or ten times less than the long ones; the long sides always corresponding to the axis of the fibre or tube, by which it is placed. The appearance of both the rounded and elongated meshes is much varied according as the vessels composing them have a straight or tortuous form. Sometimes the capillaries have a looped arrangement, a single capillary projecting from the common network into some prominent organ, and returning after forming one or more loops, as in the papillæ of the tongue and skin.

The *number* of the capillaries and the *size of the meshes* in different parts determine in general the degree of *vascularity* of those parts. The parts in which the net-work of capillaries is closest, that is, in which the meshes or interspaces are the smallest, are the lungs and the choroid membrane of the eye. In the iris and ciliary body, the interspaces are somewhat wider, yet very small. In the human liver, the interspaces are of the same size, or even smaller than the capillary vessels themselves. In the human lung they are smaller than the vessels; in the human kidney, and in the kidney of the dog, the diameter of the injected capillaries, compared with that of the interspaces, is in the proportion of one to four, or of one to three. The brain receives a very large quantity of blood; but the capillaries in which the blood is distributed through its substance are very minute, and less numerous than in some other parts. Their diameter, according to E. H. Weber, compared with the long diameter of the meshes, being in the proportion of one to eight or ten; compared with the transverse diameter, in the proportion of one to four or six. In the mucous membranes—for example, in the conjunctiva—and in the cutis vera, the capillary vessels are much larger than in the brain, and the interspaces narrower, —namely, not more than three or four times wider than the vessels. In the periosteum the meshes are much larger. In the

external coat of arteries, the width of the meshes is ten times that of the vessels (Henle).

It may be held as a general rule, that the more active the functions of an organ are, the more vascular it is; that is, the closer is its capillary network and the larger its supply of blood. Hence the narrowness of the interspaces in all glandular organs, in mucous membranes, and in growing parts; their much greater width in bones, ligaments, and other very tough and comparatively inactive tissues; and the complete absence of vessels in cartilage, and such parts as those in which, probably, very little organic change occurs after they are once formed. But the general rule must be modified by the consideration, that some organs, such as the brain, though they have small and not very closely arranged capillaries, may receive large supplies of blood by reason of its more rapid movement. When an organ has large arterial trunks and a comparatively small supply of capillaries, the movement of the blood through it will be so quick, that it may, in a given time, receive as much fresh blood as a more vascular part with smaller trunks, though at any given instant the less vascular part will have in it a smaller quantity of blood.

Fig. 110.*



In the Capillary Circulation, as seen in any transparent part of a living adult animal by means of the microscope (fig. 110), the blood flows with a constant equable motion; the red blood-corpuscles moving along, mostly in single file, and bending in various ways to accommodate themselves to the tortuous course of the capillary, but instantly recovering their normal outline on reaching a wider vessel. In very young animals, the motion, though continuous, is accelerated at intervals corresponding to the pulse in the larger arteries, and a similar motion of the blood is also seen in the capillaries of adult animals when they

* Fig. 110. Capillaries in the web of the frog's foot connecting a small artery with a small vein.

are feeble: if their exhaustion is so great that the power of the heart is still more diminished, the red corpuscles are observed to have merely the periodic motion, and to remain stationary in the intervals; while, if the debility of the animal is extreme, they even recede somewhat after each impulse, apparently because of the elasticity of the capillaries, and the tissues around them. These observations may be added to those already advanced (p. 168) to prove that, even in the state of great debility, the action of the heart is sufficient to impel the blood through the capillary vessels. Moreover, Dr. Marshall Hall having placed the pectoral fin of an eel in the field of the microscope and compressed it by the weight of a heavy probe, observed that the movement of the blood in the capillaries became obviously pulsatory, the pulsations being synchronous with the contractions of the ventricle. The pulsatory motion of the blood in the capillaries cannot be attributed to an action in these vessels; for, when the animal is tranquil, they present not the slightest change in their diameter.

It is in the capillaries, that the chief resistance is offered to the progress of the blood; for in them the friction of the blood is greatly increased by the enormous multiplication of the surface with which it is brought in contact.

At the circumference of the stream, in contact with the walls of the vessel, and adhering to them, there is a layer of *liquor sanguinis* which appears to be motionless. The existence of this *still layer*, as it is termed, is inferred both from the general fact that such an one exists in all fine tubes traversed by fluid, and from what can be seen in watching the movements of the blood-corpuscles. The red corpuscles occupy the middle of the stream and move with comparative rapidity; the colourless lymph-corpuscles run much more slowly by the walls of the vessel; while next to the wall there is often a transparent space in which the fluid appears to be at rest; for if any of the corpuscles happen to be forced within it, they move more slowly than before, rolling lazily along the side of the vessel, and often adhering to its wall. Part of this slow movement of the pale corpuscles and their occasional stoppage may be due, as E. H.

Weber has suggested, to their having a natural tendency to adhere to the walls of the vessels. Sometimes, indeed, when the motion of the blood is not strong, many of the white corpuscles collect in a capillary vessel, and for a time entirely prevent the passage of the red corpuscles.

Diapedesis of Blood-Corpuscles.

Until within the last few years it has been generally supposed that the occurrence of any transudation from the interior of the capillaries into the midst of the surrounding tissues was confined, in the absence of injury, strictly to the fluid part of the blood; in other words, that the corpuscles could not escape from the circulating stream, unless the wall of the containing blood-vessel were ruptured. It is true that an English physiologist, Dr. Augustus Waller, affirmed in 1846, that he had seen blood-corpuscles, both red and white, pass bodily through the wall of the capillary vessel in which they were contained (thus confirming what had been stated a short time previously by Dr. Addison); and that, as no opening could be seen before their escape, so none could be observed afterwards—so rapidly was the part healed. But these observations did not attract much notice until the phenomena of escape of the blood-corpuscles from the capillaries and minute veins, apart from mechanical injury, were re-discovered by Professor Cohnheim in 1867.

Fig. 111.*

Professor Cohnheim's experiment demonstrating the passage of the corpuscles through the wall of the blood-vessel, is performed in the following manner. A frog is curarized, that is to say, paralysis is produced by injecting under the skin a minute quantity of the poison called *curare;* and the abdomen having been opened, a portion of small intestine is drawn out, and its transparent mesentery spread out under a microscope. After a variable time, occupied by dilatation, following contraction, of the minute vessels, and accompanying quickening of the blood.

* *Fig.* 111. A large capillary from the frog's mesentery eight hours after irritation had been set up, showing emigration of leucocytes. *a*, cells in the act of traversing the capillary wall; *b*, some already escaped (Frey).

stream, there ensues a retardation of the current; and blood-corpuscles, both red and white, begin to make their way through the capillaries and small veins.

The *diapedesis* of the white corpuscles is thus described by Dr. Burdon-Sanderson:—

"Simultaneously with the retardation, the leucocytes, instead of loitering here and there at the edge of the axial current, begin to crowd in numbers against the vascular wall, as was long ago described by Dr. Williams. In this way the vein becomes lined with a continuous pavement of these bodies, which remain almost motionless, notwithstanding that the axial current sweeps by them as continuously as before, though with abated velocity. Now is the moment at which the eye must be fixed on the outer contour of the vessel, from which (to quote Professor Cohnheim's words) here and there minute, colourless, button-shaped elevations spring, just as if they were produced by budding out of the wall of the vessel itself. The buds increase gradually and slowly in size, until each assumes the form of a hemispherical projection, of width corresponding to that of a leucocyte. Eventually the hemisphere is converted into a pear-shaped body, the small end of which is still attached to the surface of the vein, while the round part projects freely. Gradually the little mass of protoplasm removes itself further and further away, and, as it does so, begins to shoot out delicate prongs of transparent protoplasm from its surface, in nowise differing in their aspect from the slender thread by which it is still moored to the vessel. Finally the thread is severed and the process is complete."

The process of *diapedesis* of the red corpuscles, which occurs under circumstances of impeded venous circulation, and consequently increased blood-pressure, resembles closely that of the leucocytes, with the exception that they are squeezed through the wall of the vessel and do not, like the colourless corpuscles, work their way through by active amœboid movement.

Various explanations of these remarkable phenomena have been suggested. Dr. Norris happily compares the phenomenon to the passage of a solid through a soap-bubble film, which closes up afterwards unbroken; while others believe that minute open-

ings or *stomata* between contiguous endothelial cells (p. 192), provide the means of escape for the blood corpuscles. But the chief share in the process is to be found probably in the vital endowments with respect to mobility and contraction of the parts concerned—both of the corpuscles (Bastian) and the capillary wall (Stricker). Dr. Burdon-Sanderson remarks, "the capillary is not a dead conduit, but a tube of living protoplasm. There is no difficulty in understanding how the membrane may open to allow the escape of leucocytes, and close again after they have passed out; for it is one of the most striking peculiarities of contractile substance that when two parts of the same mass are separated, and again brought into contact, they melt together as if they had not been severed."

Hitherto, the escape of the corpuscles from the interior of the blood-vessels into the surrounding tissues has been studied chiefly in connection with pathology. But it is impossible to say, at present, to what degree the discovery may not influence all present notions regarding the nutrition of the tissues, even in health.

The circulation through the capillaries must, of necessity, be largely influenced by that which occurs in the vessels on either side of them—in the arteries or the veins; their intermediate position causing them to feel at once, so to speak, any alteration in the size or rate of the arterial or venous blood-stream. Thus, the apparent contraction of the capillaries, on the application of certain irritating substances, and during fear, and their dilatation in blushing, may be referred to the action of the small arteries, rather than to that of the capillaries themselves. But largely as the capillaries are influenced by these, and by the conditions of the parts which surround and support them, their own endowments must not be disregarded. They must be looked upon, not as mere passive channels for the passage of blood, but as possessing endowments of their own, in relation to the circulation. The capillary wall is, according to Stricker, actively living and contractile; and there is no reason to doubt that, as such, it must have an important influence in connection with the blood-current.

The results of morbid action, as well as the phenomena of health, strongly support the notion of the existence of a force in the capillaries, which aids the circulation of the blood, after the same manner that nutritive fluids circulate in plants and lowly organised animals, which have no central propelling organ comparable to a heart. But this so-called *vital capillary force* occupies, in the higher animals, an entirely subordinate position.

THE VEINS.

In *structure* the coats of veins bear a general resemblance to those of arteries. Thus, they possess an *outer*, *middle*, and *internal* coat. The *outer* coat is constructed of areolar tissue like that of the arteries, but is thicker. In some veins it contains muscular fibre-cells, which are arranged longitudinally.

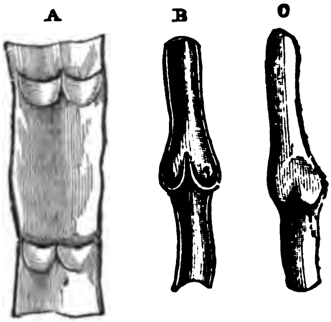
The *middle* coat is considerably thinner than that of the arteries; and, although it contains circular unstriped muscular fibres or fibre-cells, these are mingled with a larger proportion of yellow elastic and white fibrous tissue. In the large veins near the heart, namely the *venæ cavæ* and pulmonary veins, the middle coat is replaced, for some distance from the heart, by circularly arranged striped muscular fibres, continuous with those of the auricles.

The *internal* coat of veins is less brittle than the corresponding coat of an artery, but in other respects resembles it closely.

The chief influence which the veins have in the circulation, is effected with the help of the *valves*, which are placed in all veins subject to local pressure from the muscles between or near which they run. The general construction of these valves is similar to that of the semilunar valves of the aorta and pulmonary artery, already described (p. 145); but their free margins are turned in the opposite direction, *i.e. towards* the heart, so as to stop any movement of blood backward in the veins. They are commonly placed in pairs, at various distances in different veins, but almost uniformly in each (fig. 112). In the smaller veins, single valves are often met with; and three or four are sometimes placed

together, or near one another, in the largest veins, such as the subclavian, and at their junction with the jugular veins. The valves are semilunar; the unattached edge being in some examples concave, in others straight. They are composed of inextensile fibrous tissue, and are covered with epithelium like that lining the veins. During the period of their inaction, when the venous blood is flowing in its proper direction, they lie by the sides of the veins; but when in action, they close together like the valves of the arteries, and offer a complete barrier to any backward movement of the blood (figs. 113 and 114). Their situation in the superficial veins of the fore-arm is readily discovered by pressing along its surface, in a direction opposite to the venous current, *i.e.*, from the elbow towards the wrist; when little swellings (fig. 112 C) appear in the position of each pair of valves. These swellings at once disappear when the pressure is relaxed.

Fig. 112.*



Valves are not equally numerous in all veins, and in many they are absent altogether. They are most numerous in the veins of the extremities, and more so in those of the leg than the arm. They are commonly absent in veins of less than a line in diameter, and, as a general rule, there are few or none in those which are not subject to muscular pressure. Among those veins which have no valves may be mentioned the superior and inferior vena cava, the trunk and branches of the portal vein, the hepatic and renal veins, and the pulmonary veins; those in the interior of the cranium and vertebral column, those of the bones, and the

* Fig. 112. Diagrams showing valves of veins. A. Part of a vein laid open and spread out, with two pairs of valves. B. Longitudinal section of a vein, showing the apposition of the edges of the valves in their closed state. C. Portion of a distended vein, exhibiting a swelling in the situation of a pair of valves.

trunk and branches of the umbilical vein are also destitute of valves.

The principal obstacle to the circulation is already overcome when the blood has traversed the capillaries; and the force of the heart which is not yet consumed, is sufficient to complete its passage through the veins, in which the obstructions to its movement are very slight. For the formidable obstacle supposed to be presented by the gravitation of the blood, has no real existence, since the pressure exercised by the column of blood in the arteries, will be always sufficient to support a column of venous blood of the same height as itself: the two columns mutually balancing each other. Indeed, so long as both arteries and veins contain continuous columns of blood, the force of gravitation, whatever be the position of the body, can have no power to move or resist the motion of any part of the blood in any direction. The lowest blood-vessels have, of course, to bear the greatest amount of pressure; the pressure on each part being directly proportionate to the height of the column of blood above it: hence their liability to distension. But this pressure bears equally on both arteries and veins, and cannot either move, or resist the motion of, the fluid they contain, so long as the columns of fluid are of equal height in both, and continuous.

In experiments to determine what proportion of the force of the left ventricle remains to propel the blood in the veins, Valentin found that the pressure of the blood in the jugular vein of a dog, as estimated by the hæmadynamometer, did not amount to more than $\frac{1}{11}$ or $\frac{1}{12}$ of that in the carotid artery of the same animal. In the upper part of the inferior vena cava, Valentin could scarcely detect the existence of any pressure, nearly the whole force received from the heart having been, apparently, consumed during the passage of the blood through the capillaries. But slight as this remaining force might be (and the experiment in which it was estimated would reduce the force of the heart below its natural standard), it would be enough to complete the circulation of the blood; for, as already stated, the spontaneous dilatation of the auricles and ventricles, though it may not be

forcible enough to assist the movement of blood into them, is adapted to offer to that movement no obstacle.

Very effectual assistance to the flow of blood in the veins is afforded by the *action of the muscles* capable of pressing on such veins as have valves.

The *effect of muscular pressure* on such veins may be thus explained. When pressure is applied to any part of a vein, and the current of blood in it is obstructed, the portion behind the seat of pressure becomes swollen and distended as far back as to the next pair of valves. These, acting like the arterial valves, and being, like them, inextensible both in themselves and at their margins of attachment, do not follow the vein in its distension, but are drawn out towards the axis of the canal. Then, if the pressure continues on the vein, the compressed blood, tending to move equally in all directions, presses the valves down into contact at their free edges, and they close the vein and prevent regurgitation of the blood. Thus, whatever force is exercised by the pressure of the muscles on the veins, is distributed partly in pressing the blood onwards in the proper course of the circulation, and partly in pressing it backwards and closing the valves behind.

The circulation might lose as much as it gains by such compression of the veins, if it were not for the numerous anastomoses by which they communicate, one with another; for through these, the closing up of the venous channel by the backward pressure is prevented from being any serious hindrance to the circulation, since the blood, of which the onward course is arrested by the closed valves, can at once pass through some anastomosing channel, and proceed on its way by another vein (figs. 113 and 114). Thus, therefore, the effect of muscular pressure upon veins which have valves, is turned almost entirely to the advantage of the circulation; the pressure of the blood onwards is all advantageous, and the pressure of the blood backwards is prevented from being a hindrance by the closure of the valves and the anastomoses of the veins.

The effects of such muscular pressure are well shown by the acceleration of tho stream of blood when, in venesection, the

muscles of the fore-arm are put in action, and by the general acceleration of the circulation during active exercise: and the numerous movements which are continually taking place in the

Fig. 113.*

Fig. 114.†

body while awake, though their single effects may be less striking, must be an important auxiliary to the venous circulation. Yet they are not essential; for the venous circulation continues unimpaired in parts at rest, in paralysed limbs, and in parts in which the veins are not subject to any muscular pressure.

Besides the assistance thus afforded by muscular pressure to the movement of blood along veins possessed of valves, it has been discovered by Mr. Wharton Jones that, in the web of the bat's wing, the veins are furnished with valves, and possess the remarkable property of rhythmical contraction and dilatation, whereby the current of blood within them is distinctly accelerated. The contraction occurred, on an average, about ten times in a minute; the existence of valves preventing regurgitation, the entire effect of the contractions was auxiliary to the onward current of blood. Analogous phenomena have been now frequently observed in other animals.

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* Fig. 113. Vein with valves open (Dalton).

† Fig. 114. Vein with valves closed; stream of blood passing off by lateral channel (Dalton).

Agents concerned in the Circulation of the Blood.

The agents concerned in the circulation of the blood which have been now described, may be thus enumerated:—

1. The action of the heart and of the arteries.

2. The vital capillary force exercised in the capillaries.

3. The possible slight action of the muscular coat of veins; and, much more, the contraction of muscles capable of acting on veins provided with valves.

It remains only to consider (4) the influence of the respiratory movements on the circulation.

Although the continuance of the respiratory movements is essential to the circulation of the blood, and although their cessation is followed, within a very few minutes, by that of the heart's action also, yet their direct mechanical influence on the movement of the current of the blood is probably, under ordinary circumstances, but slight. The effect of expiration in increasing the pressure of the blood in the *arteries* is minutely illustrated by the experiments of Ludwig. It acts as the pressure of contracting muscles does upon the veins, and is advantageous to the onward movement of arterial blood, inasmuch as all movement backwards into the heart, which would otherwise occur at the same moment and from the same cause, is prevented by the force of the onward stream of blood from the contracting ventricle, and in the intervals of this contraction by the closure of the semilunar valves. Under ordinary circumstances, and with a free passage through the capillaries of the lungs, the effect of expiration on the stream of blood in the *veins* is also probably to assist, rather than retard its movement in the proper direction. For, with no obstruction in front, there is the force of the blood streaming into the heart from behind, to prevent any tendency to a backward flow, even apart from what may be effected by the presence of the valves of the venous system.

It is true that in *violent* expiratory efforts there is a certain retardation of the circulation in the veins. The effect of such retardation is shown in the swelling-up of the veins of the head and neck, and the lividity of the face, during coughing, straining,

and similar violent expiratory efforts; the effect shown in these instances being due both to some actual regurgitation of the blood in the great veins, and to the accumulation of blood in all the veins, from their being constantly more and more filled by the influx from the arteries.

But strong expiratory efforts, as in straining and the like, are not fairly comparable to ordinary expiration, inasmuch as they are instances of more or less interference with expiration, and involve circumstances leading to obstruction of the circulation in the pulmonary capillaries, such as are not present in the ordinary rhythmical exit of air from the lungs.

The act of *inspiration* is favourable to the venous circulation, and its effect is not counterbalanced by its tendency to draw the arterial, as well as the venous, blood towards the cavity of the chest. When the chest is enlarged in inspiration, the additional space within it is filled chiefly by the fresh quantity of air which passes through the trachea and bronchial passages to the vesicular structure of the lungs. But the blood being, like the air, subject to the atmospheric pressure, some of it also is at the same time pressed towards the expanding cavity of the chest, and therein towards the heart. The effect of this on the arterial current is hindered by the aortic valves, while they are closed, and by the forcible outward stream of blood from the ventricles when they are open; while, on the other hand, there is nothing to prevent an increased afflux of blood to the auricles through the large veins.

Sir David Barry was the first who showed plainly this effect of inspiration on the venous circulation; and he mentions the following experiment in proof of it. He introduced one end of a bent glass tube into the jugular vein of an animal, the vein being tied above the point where the tube was inserted; the inferior end of the tube was immersed in some coloured fluid. He then observed that at the time of each inspiration the fluid ascended in the tube, while during expiration it either remained stationary, or even sank. Poiseuille confirmed the truth of this observation, in a more accurate manner, by means of his hæma-dynamometer. And a like confirmation has been since furnished by Valentin, and in minute details by Ludwig.

The effect of inspiration on the veins is observable only in the large ones near the thorax. Poiseuille could not detect it by means of his instrument in veins more distant from the heart,—for example, in the veins of the extremities. And its beneficial effect would be neutralized were it not for the

valves; for he found that, when he repeated Sir D. Barry's experiments, and passed the tube so far along the veins that it went beyond the valves nearest to the heart, as much fluid was forced back into the tube in every expiration as was drawn in through it in every inspiration.

Experiments of Dr. Burdon-Sanderson have proved more directly that inspiration is favourable to the circulation, inasmuch as, during it, the tension of the arterial system is increased. And it is only when the respiratory orifice is closed, as by plugging the trachea, that inspiratory efforts are sufficient to produce an opposite effect—to *diminish* the tension in the arteries.

On the whole, therefore, the respiratory movements of the chest are advantageous to the circulation.

Velocity of the Circulation.

The velocity of the blood-current at any given point in the various divisions of the circulatory system is inversely proportional to their sectional area at that point. If, as Professor Müller says, the sectional area of all the branches of a vessel united were always the same as that of the vessel from which they arise, and if the aggregate sectional area of the capillary vessels were equal to that of the aorta, the mean rapidity of the blood's motion in the capillaries would be the same as in the aorta and largest arteries; and if a similar correspondence of capacity existed in the veins and arteries, there would be an equal correspondence in the rapidity of the circulation in them. But the arterial and venous systems may be represented by two truncated cones with their apices directed upwards, *i.e.* towards the heart; the area of their united bases (the sectional area of the capillaries) being 400—500 times as great as that of the truncated apex representing the aorta. Thus the velocity of blood in the capillaries is about $\frac{1}{400}$ of that in the aorta.

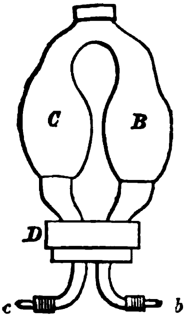
Velocity of the Blood in the Arteries.

The velocity of the stream of blood is greater in the arteries than in any other part of the circulatory system, and in them it is greatest in the neighbourhood of the heart, and during the ventricular systole; the rate of movement diminishing during the diastole of the ventricles, and in the parts of the arterial system most distant from the heart. Chauveau has estimated the

rapidity of the blood-stream in the carotid of the horse at about 20 inches per second during the heart's systole, and nearly 9 inches during the diastole.

Various instruments have been devised for measuring the velocity of the blood-stream in the arteries.

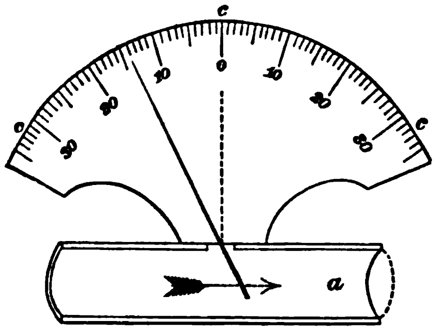
Fig. 115.*



Ludwig's "Stromuhr" (fig. 115) consists of an U-shaped tube dilated at B and C, and whose extremities, *b* and *c*, are inserted into an artery. At the commencement of the experiment, *c* being directed towards the heart, C is filled with olive oil, and B with defibrinated blood. The capacity of C being known, the quantity of blood which passes through the artery in a given time may be estimated from the period occupied in displacing the contents of C into B. The tube C having now become full of blood, and B full of oil, the two tubes are, by means of a mechanical arrangement at D, twisted round so as to change places with reference to *b* and *c*, and the experiment may be repeated.

Chauveau's instrument (fig. 116) consists of a thin brass tube, *a*, in one side of which is a small perforation closed by thin vulcanized indiarubber. Passing through the rubber is a fine lever, one end of which, slightly flattened, extends into the *lumen*

Fig. 116.†



of the tube, while the other moves over the face of a dial. The tube is inserted into the interior of an artery, and ligatures applied to fix it, so that the movement of the blood may, in flowing through the tube, be indi-

* Fig. 115. Ludwig's "Stromuhr."

† Fig. 116. Chauveau's instrument. *a*, Brass tube introduced into the lumen of the artery, and containing an index-needle, which passes through the elastic membrane in its side, and moves by the impulse of the blood current. *c*, Graduated scale, for measuring the extent of the oscillations of the needle.

cated by the movement of the outer extremity of the lever on the face of the dial.

The Hæmatochometer of Vierordt, and the instrument of M. Lortet, resemble in principle that of M. Chauveau.

Velocity of the Blood in the Capillaries.

The observations of Hales, E. H. Weber, and Valentin agree very closely as to the rate of the blood-current in the capillaries of the frog; and the mean of their estimates gives the velocity of the *systemic* capillary circulation at about one inch per minute. Through the *pulmonic* capillaries the rate of motion, according to Hales, is about five times that through the systemic ones. The velocity in the capillaries of warm-blooded animals is greater. If it be assumed to be three times as great as in the frog, still the estimate may seem too low, and inconsistent with the facts, which show that the whole circulation is accomplished in about a minute. But the whole length of capillary vessels, through which any given portion of blood has to pass, probably does not exceed $\frac{1}{50}$th of an inch; and therefore the time required for each quantity of blood to traverse its own appointed portion of the general capillary system will scarcely amount to a second: while in the pulmonic capillary system the length of time required will be much less even than this. These estimates are taken from observations of the movements of the red corpuscles in the centre of the stream.

Velocity of Blood in the Veins.

The *velocity* of the blood is greater in the veins than in the capillaries, but less than in the arteries: this fact depending upon the relative capacities of the arterial and venous systems. If an accurate estimate of the proportionate areas of arteries and the veins corresponding to them could be made, we might, from the velocity of the arterial current, calculate that of the venous. An usual estimate is, that the capacity of the veins is about twice or three times as great as that of the arteries, and that the velocity of the blood's motion is, therefore, about twice or three times as great in the arteries as in the veins. Some doubt has, however, been lately expressed regarding the accuracy of

this calculation, and the matter, therefore, must be considered not yet settled. The rate at which the blood moves in the veins gradually increases the nearer it approaches the heart, for the sectional area of the venous trunks, compared with that of the branches opening into them, becomes gradually less as the trunks advance towards the heart.

Velocity of the Circulation as a Whole.

Having now considered the share which each of the circulatory organs has in the propulsion and direction of the blood, we may speak of their combined effects, especially in regard to the velocity with which the movement of the blood through the whole round of the circulation is accomplished.

From the rate at which the blood escapes from opened vessels we can only judge, in general, that its velocity is, as already said, greater in arteries than in veins, and in both these greater than in the capillaries. But it is evident, as Müller remarks, that its rate of movement in the vessels cannot be calculated from this, insomuch as, in the closed vessels, no portion of blood can be moved forwards except by moving what is in front of it. More satisfactory data for the estimates are afforded by the results of experiments to ascertain the rapidity with which poisons introduced into the blood are transmitted from one part of the vascular system to another. From eighteen such experiments on horses, Hering deduced that the time required for the passage of a solution of ferrocyanide of potassium, mixed with the blood, from one jugular vein (through the right side of the heart, the pulmonary circulation, the left cavities of the heart, and the general circulation) to the jugular vein of the opposite side, varies from twenty to thirty seconds. The same substance was transmitted from the jugular vein to the great saphena in twenty seconds; from the jugular vein to the masseteric artery, in between fifteen and thirty seconds; to the facial artery, in one experiment, in between ten and fifteen seconds; in another experiment in between twenty and twenty-five seconds; in its transit from the jugular vein to the metatarsal artery, it occupied between twenty and thirty seconds, and in one instance more

than forty seconds. The result was nearly the same whatever was the rate of the heart's action.

Poiseuille's observations accord completely with the above, and show, moreover, that when the ferrocyanide is injected into the blood with other substances, such as acetate of ammonia, or nitrate of potash (solutions of which, as other experiments have shown, pass quickly through capillary tubes), the passage from one jugular vein to the other is effected in from eighteen to twenty-four seconds; while, if instead of these, alcohol is added, the passage is not completed until from forty to forty-five seconds after injection. Still greater rapidity of transit has been observed by Mr. J. Blake, who found that nitrate of baryta injected into the jugular vein of a horse could be detected in blood drawn from the carotid artery of the opposite side in from fifteen to twenty seconds after the injection. In sixteen seconds a solution of nitrate of potash, injected into the jugular vein of a horse, caused complete arrest of the heart's action, by entering and diffusing itself through the coronary arteries. In a dog, the poisonous effects of strychnia on the nervous system were manifested in twelve seconds after injection into the jugular vein; in a fowl, in six and a half seconds, and in a rabbit in four and a half seconds.

In all these experiments, it is assumed that the substance injected moves with the blood, and at the same rate as it, and does not move from one part of the organs of circulation to another by diffusing itself through the blood or tissues more quickly than the blood moves. The assumption is sufficiently probable, to be considered nearly certain, that the times above-mentioned, as occupied in the passage of the injected substances, are those in which the portion of blood, into which each was injected, was carried from one part to another of the vascular system. It would, therefore, appear that a portion of blood can traverse the entire course of the circulation, in the horse, in half a minute; of course it would require longer to traverse the vessels of the most distant part of the extremities than to go through those of the neck; but taking an average length of vessels to be traversed, and assuming, as we may, that the move-

ment of blood in the human subject is not slower than in the horse, it may be concluded that one minute, which is the estimate usually adopted of the average time in which the blood completes its entire circuit in man, is above rather than below the actual rate.

Another mode of estimating the general velocity of the circulating blood, is by calculating it from the quantity of blood supposed to be contained in the body, and from the quantity which can pass through the heart in each of its actions. But the conclusions arrived at by this method are less satisfactory. For the estimates both of the total quantity of blood, and of the capacity of the cavities of the heart, have as yet only approximated to the truth. Still the most careful of the estimates thus made accord with those already mentioned; and it may be assumed that the blood may all pass through the heart in from twenty-five to fifty seconds.

The estimate of the speed at which the blood may be seen moving in transparent parts, is not opposed to this. For, as already stated (p. 209), though the movement through the capillaries may be very slow, yet the length of capillary vessel through which any portion of blood has to pass is very small.

All the estimates here given are averages; but of course the time in which a given portion of blood passes from one side of the heart to the other, varies much according to the organ it has to traverse. The blood which circulates from the left ventricle, through the coronary vessels, to the right side of the heart, requires a far shorter time for the completion of its course than the blood which flows from the left side of the heart to the feet, and back again to the right side of the heart; for the circulation from the left to the right cavities of the heart may be represented as forming a number of arches, varying in size, and requiring proportionately various times for the blood to traverse them; the smallest of these arches being formed by the circulation through the coronary vessels of the heart itself. The course of the blood from the right side of the heart, through the lungs to the left, is shorter than most of the arches described by the systemic circulation, and in it the blood flows, *cæteris paribus*, much quicker than

in most of the vessels which belong to the aortic circulation. For although the quantity of blood contained, at any instant, in the *systemic* circulation of the body, is far greater than the quantity within the *pulmonary* circulation; yet, in any given space of time, as much blood must pass through the lungs as passes in the same time through the systemic circulation. If the systemic vessels contain five times as much blood as the pulmonary, the blood in them must move five times as slow as in these; else, the right side of the heart would be either overfilled or not filled enough.

Peculiarities of the Circulation in different Parts.

The most remarkable peculiarities attending the circulation of blood through different organs are observed in the cases of the *lungs*, the *liver*, the *brain*, and the *erectile organs*. The pulmonary and portal circulations have been already alluded to (pp. 135, 136), and will be again noticed when considering the functions of the lungs and liver.

The chief circumstances requiring notice, in relation to the *cerebral circulation*, are observed in the arrangement and distribution of the vessels of the brain, and in the conditions attending the amount of blood usually contained within the cranium.

For the due performance of its functions, the brain requires a large supply of blood. This is accomplished through the number and size of its arteries, the two internal carotids, and the two vertebrals. But it appears to be further necessary that the force with which this blood is sent to the brain should be less, or at least, subject to less variation from external circumstances than it is in other parts. This object is effected by several provisions; such as the tortuosity of the large arteries, and their wide anastomoses in the formation of the circle of Willis, which will insure that the supply of blood to the brain may be uniform, though it may by an accident be diminished, or in some way changed, through one or more of the principal arteries. The transit of the large arteries through bone, especially the carotid canal of the temporal bone, may prevent any undue distension; and uniformity of supply is further insured by the arrangement of the vessels in the pia mater, in which, previous to their distribution to the substance of the brain, the large arteries break up and divide into innumerable minute branches ending in capillaries, which, after frequent communications with one another, enter the brain, and carry into nearly every part of it uniform and equable streams of blood.

The arrangement of the *veins* within the cranium is also peculiar. The large venous trunks or sinuses are formed so as to be scarcely capable of change of size; and composed, as they are, of the tough tissue of the dura mater, and, in some instances, bounded on one side by the bony cranium, they are not compressible by any force which the fulness of the arteries might exercise through the substance of the brain; nor do they admit of distension when the flow of venous blood from the brain is obstructed.

The general uniformity in the supply of blood to the brain, which is thus secured, is well adapted, not only to its functions, but also to its condition as a mass of nearly incompressible substance placed in a cavity with unyielding walls. These conditions of the brain and skull have appeared, indeed, to some, enough to justify the opinion that the quantity of blood in the brain must be at all times the same. But Sir G. Burrows found that in animals bled to death, without any aperture being made in the cranium, the brain became pale and anæmic like other parts. And in proof that, during life, the cerebral circulation is influenced by the same general circumstances that influence the circulation elsewhere, he found congestion of the cerebral vessels in rabbits killed in strangling or drowning; while in others, killed by prussic acid, he observed that the quantity of blood in the cavity of the cranium was determined by the position in which the animal was placed after death, the cerebral vessels being congested when the animal was suspended with its head downwards, and comparatively empty when the animal was kept suspended by the ears. He concluded, therefore, that although the total volume of the contents of the cranium is probably nearly always the same, yet the quantity of blood in it is liable to variation, its increase or diminution being accompanied by a simultaneous diminution or increase in the quantity of the cerebro-spinal fluid, which, by readily admitting of being removed from one part of the brain and spinal cord to another, and of being rapidly absorbed, and as readily effused, would serve as a kind of supplemental fluid to the other contents of the cranium, to keep it uniformly filled in case of variations in their quantity. And there can be no doubt that, although the arrangements of the blood-vessels, to which reference has been made, ensure to the brain an amount of blood which is tolerably uniform, yet, inasmuch as with every beat of the heart and every act of respiration, and under many other circumstances, the quantity of blood in the cavity of the cranium is constantly varying, it is plain that, were there not provision made for the possible displacement of some of the contents of the unyielding bony case in which the brain is contained, there would be often alternations of excessive pressure with insufficient supply of blood. Hence we may consider that the cerebro-spinal fluid in the interior of the skull not only subserves the mechanical functions of fat in other parts as a *packing* material, but by the readiness with which it can be displaced into the spinal canal, provides the means whereby undue pressure and insufficient supply of blood are equally prevented.

Circulation in erectile structures.—The instances of greatest variation in the quantity of blood contained, at different times, in the same organs, are found in certain structures which, under ordinary circumstances, are soft and flaccid, but, at certain times, receive an unusually large quantity of blood, become distended and swollen by it, and pass into the state which has been termed *erection*. Such structures are the corpora cavernosa and corpus spongiosum of the penis in the male, and the clitoris in the female; and, to a less degree, the nipple of the mammary gland in both sexes. The corpus cavernosum penis, which is the best example of an erectile structure, has an external fibrous membrane or sheath; and from the inner surface of the latter are prolonged numerous fine lamellæ which divide its cavity into small compartments looking like cells when they are inflated. Within these is situated the plexus of veins upon which the peculiar erectile property of

the organ mainly depends. It consists of short veins which very closely interlace and anastomose with each other in all directions, and admit of great variation of size, collapsing in the passive state of the organ, but, for erection, capable of an amount of dilatation which exceeds beyond comparison that of the arteries and veins which convey the blood to and from them. The strong fibrous tissue lying in the intervals of the venous plexuses, and the external fibrous membrane or sheath with which it is connected. limit the distension of the vessels, and, during the state of erection, give to the penis its condition of tension and firmness. The same general condition of vessels exists in the corpus spongiosum urethræ, but around the urethra the fibrous tissue is much weaker than around the body of the penis, and around the glans there is none. The venous blood is returned from the plexuses by comparatively small veins; those from the glans and the fore part of the urethra empty themselves into the dorsal vein of the penis; those from the corpus cavernosum pass into deeper veins which issue from the corpora cavernosa at the crura penis; and those from the rest of the urethra and bulb pass more directly into the plexus of the veins about the prostate. For all these veins one condition is the same; namely, that they are liable to the pressure of muscles when they leave the penis. The muscles chiefly concerned in this action are the erector penis and accelerator urinæ.

Erection results from the distension of the venous plexuses with blood. The principal exciting cause in the erection of the penis is nervous irritation, originating in the part itself, or derived from the brain and spinal cord. The nervous influence is communicated to the penis by the pudic nerves, which ramify in its vascular tissue: and Guenther has observed, that, after their division in the horse, the penis is no longer capable of erection. It affords a good example of the subjection of the circulation in an individual organ to the influence of the nerves; but the mode in which they excite a greater influx of blood is not with certainty known.

The most probable explanation is that offered by Professor Kölliker, who ascribes the distension of the venous plexuses to the influence of organic muscular fibres, which are found in abundance in the corpora cavernosa of the penis, from the bulb to the glans, also in the clitoris and other parts capable of erection. While erectile organs are flaccid and at rest, these contractile fibres exercise an amount of pressure on the plexuses of vessels distributed amongst them, sufficient to prevent their distension with blood. But when through the influence of their nerves, these parts are stimulated to erection, the action of these fibres is suspended, and the plexuses thus liberated from pressure, yield to the distending force of the blood, which, probably, at the same time arrives in greater quantity, owing to a simultaneous dilatation of the arteries of the parts, and thus the plexuses become filled, and remain so until the stimulus to erection subsides, when the organic muscular fibres again contract, and so gradually expel the excess of blood from the previously distended vessels. The influence of cold in producing extreme contraction and shrinking of erectile organs, and the opposite effect of warmth in inducing fulness and distension of these parts, are among the arguments used by Kölliker in support of this opinion.

The accurate dissections and experiments of Kobelt, extending and confirming those of Le Gros Clark and Krause, have shown, that this influx of the blood, however explained, is the first condition necessary for erection,

and that through it alone much enlargement and turgescence of the penis may ensue. But the erection is probably not complete, nor maintained for any time except when, together with this influx, the muscles already mentioned contract, and by compressing the veins, stop the efflux of blood, or prevent it from being as great as the influx.

It appears to be only the most perfect kind of erection that needs the help of muscles to compress the veins; and none such can materially assist the erection of the nipples, or that amount of turgescence, just falling short of erection, of which the spleen and many other parts are capable. For such turgescence nothing more seems necessary than a large plexiform arrangement of the veins, and such arteries as may admit, upon occasion, augmented quantities of blood.

CHAPTER VIII.

RESPIRATION.

THE maintenance of animal life necessitates the continual absorption of oxygen and excretion of carbonic acid; the blood being, in all animals which possess a well developed blood vascular system, the medium by which these gases are carried. By the blood, oxygen is absorbed from without and conveyed to all parts of the organism; and, by the blood, carbonic acid, which comes from within, is carried to those parts by which it may escape from the body. The two processes,—absorption of oxygen and excretion of carbonic acid,—are complementary, and their sum is termed the process of *Respiration*.

Under the head of respiration are frequently included the absorption and exhalation of other matters than carbonic acid and oxygen. But, excepting watery vapour, which is so constantly exhaled by the lungs as to deserve to be included with carbonic acid, as an essential respiratory product, in air-breathing animals, all other gaseous matters than those just referred to must be considered accessory or accidental rather than essential.

In all Vertebrata, and in a large number of Invertebrata, certain parts (either lungs or gills) are specially constructed for bringing the blood into proximity with the aerating medium (atmospheric air, or water containing air in solution).

In some of the lower vertebrata (frogs and other naked amphibia) the skin is important as a respiratory organ, and is capable of supplementing, to some extent, the functions of the proper breathing apparatus; but in all the higher animals, including man, the respiratory capacity of the skin is so infinitesimal that it may be practically disregarded.

Essentially, a lung or gill is constructed of a fine transparent membrane, one surface of which is exposed to the air or water as the case may be, while, on the other, is a network of blood-vessels,—the only separation between the blood and aerating medium being the thin wall of the blood-vessels, and the fine membrane, on one side of which vessels are distributed. The difference between the simplest and the most complicated respiratory membrane is one of degree only. The apparently complex lung of a bird or mammal is but a bag or sac, the walls of which are extensively folded and re-folded in order to obtain, in a given space, the greatest possible amount of aerating surface; and thus, to the naked eye, such a lung on section looks like a solid organ. A lung, such as this, is not less an air-containing sac than is the lung of the frog, the walls of which are not infolded sufficiently to interfere with its bag-like appearance.

The various complexity of the respiratory membrane, and the kind of aerating medium (whether air or water), are not the only conditions which cause a difference in the respiratory capacity of different animals. The number and size of the red blood-corpuscles (*respiratory cells*, as they have been termed), the mechanism of the breathing apparatus, the presence or absence of a *pulmonary* heart physiologically distinct from the *systemic*, are, all of them, conditions scarcely second in importance.

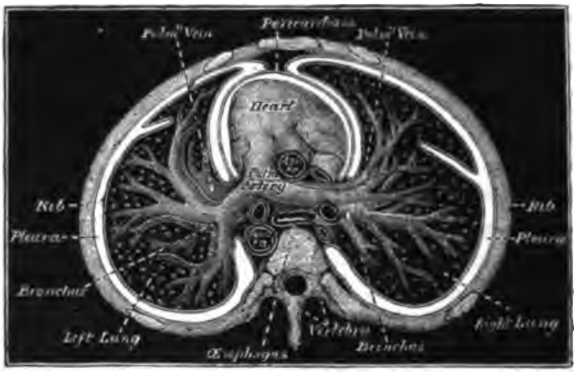
It may be well to state here that the lungs are only the medium for the *exchange*, on the part of the blood, of carbonic acid for oxygen. They are not the seat in any special manner, of those combustion-processes, of which the production of carbonic acid is the final result. These occur in all parts of the body—more in one part, less in another; partly in the substance of the tissues, partly in the capillary blood-vessels contained in them.

Position and Structure of the Lungs.

The lungs occupy the greater portion of the chest, or uppermost of the two cavities into which the body is divided by the diaphragm (fig. 71). They are of a spongy elastic texture, and on section appear to the naked eye as if they were in great part solid organs, except here and there, at certain points, where branches of the bronchi or air-tubes may have been cut across, and show, on the surface of the section, their tubular structure.

In fact, however, the lungs are hollow organs, and we may consider them as really two bags containing air, each of which communicates by a separate orifice with a common air-tube, the *trachea* (fig. 118), through the upper portion of which, the *larynx*, they freely communicate with the external atmosphere. The

Fig. 117.*



orifice of the larynx is guarded by muscles, and can be opened or closed at will.

Each lung is enveloped by a serous membrane—the ***pleura***, one layer of which adheres closely to the surface of the lung, and provides it with its smooth and slippery covering, while the other adheres to the inner surface of the chest-wall. The continuity of the two layers, which form a closed sac, as in the case of other serous membranes, will be best understood by reference

* Fig. 117. Transverse section of the chest (after Gray).

to fig. 117. The appearance of a space, however, between the pleura which covers the lung (*visceral* layer), and that which lines the inner surface of the chest (*parietal* layer), is inserted in the drawing only for the sake of distinctness. These layers are, in health, everywhere in contact, one with the other; and between them is only just so much fluid as will ensure the lungs gliding easily on the inner surface of the parietal layer, which lines the chest-wall. While considering the subject of normal respiration, we may discard altogether the notion of the existence of any space or cavity between the lung and the wall of the chest. So far as the movement of the lungs is concerned they might be adherent to the chest-wall, inasmuch as they accompany the latter in all its movements.

If, however, an opening be made so as to permit air or fluid to enter the pleural sac, the lung, in virtue of its elasticity, recoils, and a considerable space is left between the lung and the chest-wall. In other words, the natural elasticity of the lungs would cause them at all times to contract away from the ribs, were it not that the contraction is resisted by atmospheric pressure which bears only on the *inner* surface of the air-tubes and air-cells. On the admission of air into the pleural sac, atmospheric pressure bears alike on the inner and outer surfaces of the lung, and their elastic recoil is thus no longer prevented.

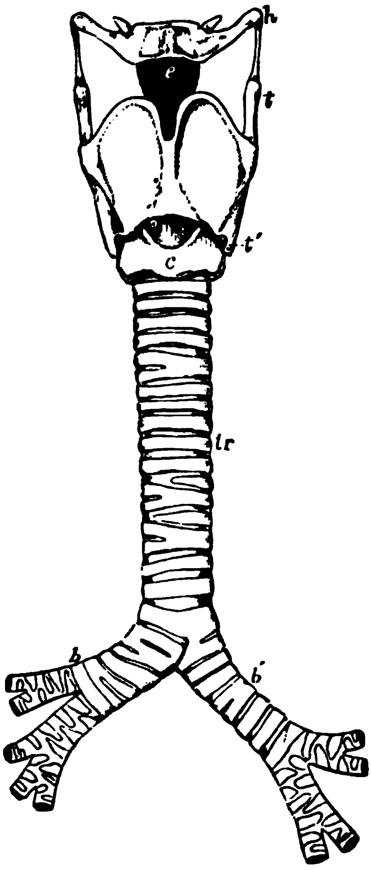
The structure of the pleura closely resembles that of othér serous membranes. It is covered with a delicate layer of polygonal epithelial cells. Usually these are of a flattened scaly form, but their shape varies according to the degree of distension of the lung. In the pulmonary pleura of a *collapsed* lung they are found to be of a spheroidal, or even columnar form, while if the lung be fully inflated, they at once become thin and flattened (Klein). These alterations of shape are the necessary consequence of the varying area which the cells have to cover.

Scattered bundles of unstriped muscular fibre occur in the pulmonary pleura. They are especially strongly developed on those parts (anterior and internal surfaces of lungs) which move most freely in respiration: their function is doubtless to aid in expiration (Klein)

Structure of the Trachea and Bronchial Tubes.

The *trachea* or windpipe extends from the cricoid cartilage, which is on a level with the fifth cervical vertebra, to a point opposite the third dorsal vertebra, where it divides into the two bronchi, one for each lung (fig. 118). It measures, on an average, four or four-and-a-half inches in length, and from three-quarters of an inch to an inch in diameter.

Fig. 118.*



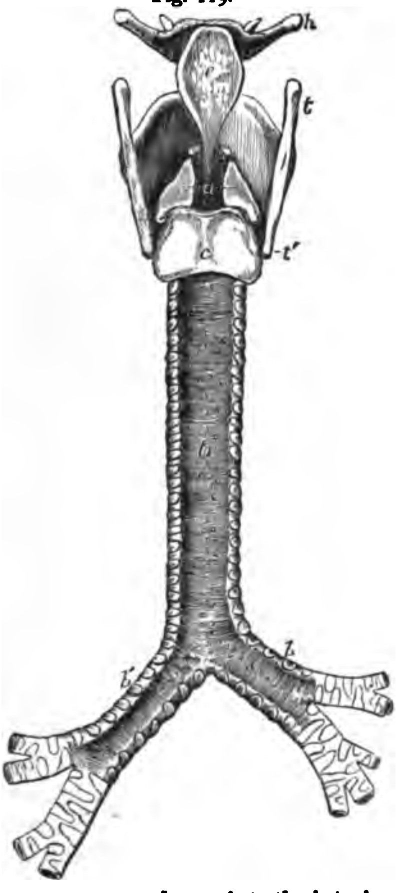
The trachea is essentially a tube of fibro-elastic membrane, within the layers of which are enclosed a series of cartilaginous rings, from sixteen to twenty in number. These rings extend only around the front and sides of the trachea (about two-thirds of its circumference), and are deficient behind; the interval between their posterior extremities being bridged over by a continuation of the fibrous membrane in which they are enclosed (fig. 119).

Immediately within this fibro-cartilaginous tube, at the back, is a layer of unstriped muscular fibres, which extends, *transversely*, between the

* Fig. 118. Outline showing the general form of the larynx, trachea, and bronchi, as seen from before. *h*, the great cornu of the hyoid bone; *e*, epiglottis; *t*, superior, and *t'*, inferior cornu of the thyroid cartilage; *c*, middle of the cricoid cartilage; *tr*, the trachea, showing sixteen cartilaginous rings; *b*, the right, and *b'*, the left bronchus. (Allen Thomson.) ½.

ends of the cartilaginous rings to which they are attached, and opposite the intervals between them, also; their evident function being to diminish, when required, the calibre of the trachea by approximating the ends of the cartilages. Outside these are a few *longitudinal* bundles of muscular tissue, which, like the preceding, are attached both to the fibrous and cartilaginous framework.

Fig. 119.*



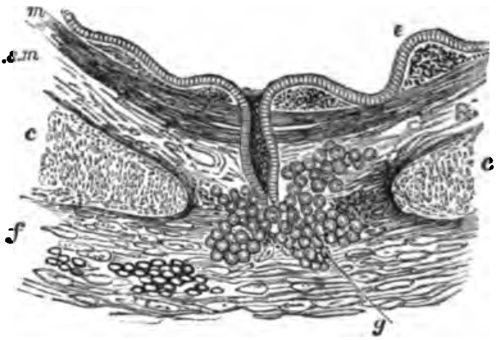
The trachea is lined by mucous membrane, the epithelium of which is columnar and ciliated (fig. 122); while immediately outside the mucous membrane and adhering closely to it, are numerous longitudinal bundles of yellow elastic tissue.

Numerous mucous glands are situate on the exterior and in the substance of the fibrous framework of the trachea; their ducts perforating the various structures which form the wall of the trachea, and opening through the mucous membrane into the interior.

* Fig. 119. Outline showing the general form of the larynx, trachea, and bronchi as seen from behind. *h*, great cornu of the hyoid bone; *t*, superior, and *t'*, the inferior cornu of the thyroid cartilage; *e*, the epiglottis; *a*, points to the back of both the arytenoid cartilages, which are surmounted by the cornicula; *c*, the middle ridge on the back of the cricoid cartilage; *tr*, the posterior membranous part of the trachea; *b*. *b'*, right and left bronchi. (Allen Thomson.) ½.

The two bronchi into which the trachea divides, of which the right is shorter, broader, and more horizontal than the left (fig. 118), resemble the trachea exactly in structure, and in the arrangement of their cartilaginous rings. On entering the

Fig. 120.*



substance of the lungs, however, the rings, although they still form only larger or smaller segments of a circle, are no longer confined to the front and sides of the tubes, but are distributed impartially to all parts of their circumference.

The bronchi divide and sub-divide in the substance of the lungs, into a number of smaller and smaller branches, which penetrate into every part of the organ, until at length they end in the smaller sub-divisions of the lung called *lobules*.

All the larger branches still have walls formed of tough membrane, containing portions of cartilaginous rings, by which they are held open, and unstriped muscular fibres, as well as longitudinal bundles of elastic tissue. They are lined by mucous membrane, the surface of which, like that of the larynx and trachea, is covered with vibratile ciliary epithelium (fig. 122). The mucous membrane is abundantly provided with mucous glands.

* Fig. 120. Transverse section of a bronchus, about ¼ inch in diameter (F. E. Schulze). *e*, Epithelium (ciliated); immediately beneath it is the mucous membrane or internal fibrous layer, of varying thickness; *m*, Muscular layer; *s m*, Fibrous tissue; *f*, Fibrous tissue; *c*, Cartilage enclosed within the layers of fibrous tissue; *g*, Mucous gland.

As the bronchi become smaller and smaller, and their walls thinner, the cartilaginous rings become scarcer and

Fig. 121.*

more irregular, until, in the smaller bronchial tubes, they are represented only by minute and scattered cartilaginous flakes. And when the bronchi, by successive branches, are reduced to about $\frac{1}{40}$ of an inch in diameter, they lose their cartilaginous element altogether, and their walls are formed only of a tough fibrous elastic membrane, with circular muscular fibres; they are still lined, however, by a thin mucous membrane, with ciliated epithelium. In the smaller bronchi the circular muscular fibres are more abundant than in the trachea and larger bronchi, and form a distinct circular coat.

Structure of the Lungs.

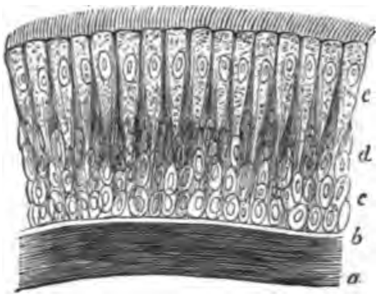
Each lung is partially subdivided into separate portions, called

---

* Fig. 121. A diagrammatic representation of the heart and great vessels in connection with the lungs—¼. The pericardium has been removed, and the lungs are turned aside. 1, right auricle; 2, vena cava superior; 3, vena cava inferior; 4, right ventricle; 5, stem of the pulmonary artery; *a a*, its right and left branches; 6, left auricular appendage; 7, left ventricle; 8, aorta; 9, 10, the two lobes of the left lung; 11, 12, 13, the three lobes of the right lung; *b b*, right and left bronchi; *v v*, right and left upper pulmonary veins.

lobes; the right lung into three lobes, and the left into two (fig. 121). Each of these lobes, again, is composed of a large number of minute parts, called *lobules*. Each pulmonary lobule may be considered a lung in miniature, consisting, as it does, of a branch of the bronchial tube, of air-cells, blood-vessels, nerves and lymphatics, with a sparing amount of areolar tissue.

Fig. 122.*



On entering a lobule, the small bronchial tube (*a*, fig. 123) divides and subdivides; its walls, at the same time, becoming thinner and thinner, until at length they are formed only of a thin membrane of areolar and elastic tissue, lined by a layer of *squamous* epithelium, not provided with cilia. At the same time, they are altered in shape; each of the minute terminal branches widening out funnel-wise, and its walls being pouched out irregularly into small saccular dilatations, called *air-cells* (fig. 123, *b*). Such a funnel-shaped terminal branch of the bronchial tube, with its group of pouches or air-cells, has been called an *infundibulum* (figs. 123, 124), and the irregular oblong space in its centre, with which the air-cells communicate, an *intercellular passage*.

Fig. 123.†

* Fig. 122. Ciliary epithelium of the human trachea magnified 350 diameters. *a*, Layer of longitudinally arranged elastic fibres; *b*, Basement membrane; *c*, Deepest cells, circular in form; *d*, Intermediate elongated cells; *e*, Outermost layer of cells fully developed and bearing cilia (Kölliker).

† Fig. 123. Terminal branch of a bronchial tube, with its infundibula and air-cells, from the margin of the lung of a monkey, injected with quicksilver. *a*, Terminal bronchial twig; *b b*, infundibula and air-cells. × 10. (F. E. Schulze.)

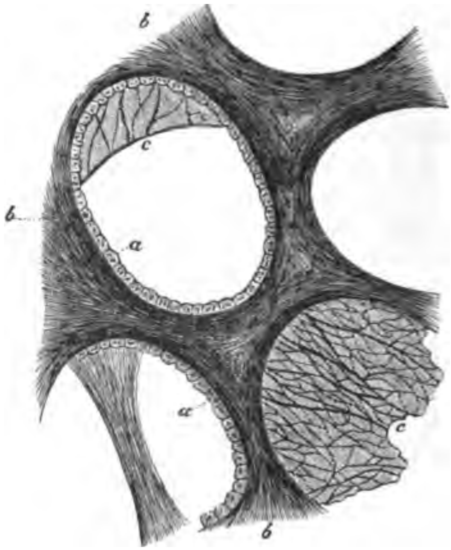
The air-cells may be placed singly, like recesses from the intercellular passage, but more often they are arranged in groups or even in rows, like minute sacculated tubes; so that a short series of cells, all communicating with one another, open by a common orifice into the tube. The cells are of various forms, according to the mutual pressure to which they are subject; their walls are nearly in contact, and they vary from $\frac{1}{50}$ to $\frac{1}{70}$ of an inch in diameter. Their walls are formed of fine membrane, similar to that of the intercellular passages, and continuous with it, which membrane is folded on itself so as to form a sharp-edged border at each circular orifice of communication between contiguous air-cells, or between the cells and the bronchial passages. Numerous fibres of elastic tissue are spread out between contiguous air-cells, and many of these are attached to the outer surface of the fine membrane of which each cell is composed, imparting to it additional strength, and the power of recoil after distension (fig. 125, *b* and *c*). The cells are lined by a layer of *squamous* or *tessellated* epithelium, not provided with cilia. Outside the cells, a network of pulmonary capillaries is spread out so densely (fig. 126), that the interspaces or meshes are even narrower than the vessels, which are, on an average, $\frac{1}{3000}$ of an inch in diameter. Between the atmospheric air in the cells and the blood in these vessels, nothing intervenes but the thin walls of the cells and capillaries; and the exposure of the blood to the air is the more complete, because the folds of membrane between contiguous cells, and often the spaces between the walls of the same, contain only a single

Fig. 124.*

* Fig. 124. Two small groups of air-cells, or *infundibula*, *a a*, with air-cells, *b b*, and the ultimate bronchial tubes, *c c*, with which the air-cells communicate. From a new-born child (Kölliker).

layer of capillaries, both sides of which are thus at once exposed to the air.

Fig. 125.*



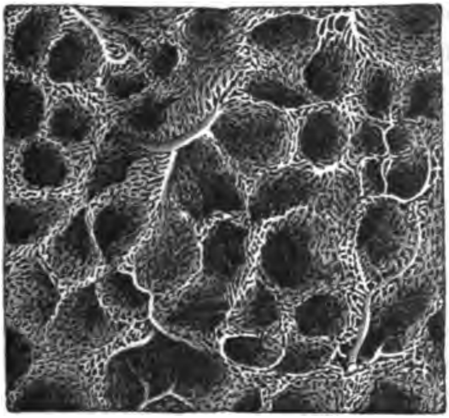
The cells situated nearest to the centre of the lung are smaller, and their networks of capillaries are closer than those nearer to the circumference. The cells of adjacent lobules do not communicate; and those of same lobule, or proceeding from the same intercellular passage, do so as a general rule only near angles of bifurcation; so that, when any bronchial tube is closed or obstructed, the supply of air is lost for all the cells opening into it or its branches.

The lungs receive blood from two sources, (*a*) the pulmonary artery, (*b*) the bronchial arteries. The former, it need scarcely be said, conveys venous blood to the lungs in order to its arterialization, and this blood takes no share in the nutrition of the pulmonary tissues through which it passes. (*b*) The branches of

* Fig. 125. Air-cells of lung, magnified 350 diameters. *a*, Epithelial lining of the cells; *b*, Fibres of elastic tissue; *c*, Delicate membrane of which the cell-wall is constructed, with elastic fibres attached to it (Kölliker).

the bronchial arteries ramify for nutrition's sake in the walls of the bronchi, of the larger pulmonary vessels, in the interlobular connective tissue, &c.; the blood of the bronchial vessels being

Fig. 126.*



returned, partly through the bronchial and partly through the pulmonary veins.

The lung is abundantly supplied with lymphatics.

According to the researches of Dr. Klein, the lymphatics are arranged in three sets :—

1. Irregular lacunæ in the walls of the alveoli, or air-cells. The lymphatic vessels which lead from these, accompany the pulmonary vessels towards the root of the lung.

2. Irregular anastomosing spaces in the walls of the bronchi.

3. Lymph-spaces in the pulmonary pleura. The lymphatic vessels from all these irregular sinuses pass in towards the root of the lung to reach the bronchial glands.

The nerves of the lung are to be traced from the anterior and posterior pulmonary plexuses, which are formed by branches both of the vagus and sympathetic. The nerves follow the course of the vessels and bronchi, and in the walls of the latter many small ganglia are situated.

* Fig. 126. Capillary net-work of the pulmonary blood-vessels in the human lung (Kölliker). × 60.

Mechanism of Respiration.

The act of respiration consists of the alternate expansion and contraction of the walls of the chest, by which air is alternately drawn into and expelled from its interior. For the proper understanding of the mechanism by which these movements are effected, the following facts must be borne in mind.

The lungs form two distinct hollow bags, communicating with the exterior of the body by an air-tube common to both (trachea and larynx, fig. 118), and are always closely in contact with the inner surface of the chest walls, while their lower portions are closely in contact with the diaphragm or muscular partition which separates the chest from the abdomen. The lungs follow all movements of the parts in contact with them; and for the evident reason that the outer surface of the lung-bag not being exposed directly to atmospheric pressure, while the inner surface is so exposed, the pressure from within preserves the lungs in close contact with the parts surrounding them, and obliterates, practically, the pleural space, and must continue to do so, until from some cause or other—say from an opening for the admission of air through the chest walls, the pressure on the outside of the lung equals or exceeds that on the interior. Any such artificial condition of things, however, need not here be considered.

For the *inspiration* of air into the lungs it will be evident from the foregoing facts, that all that is necessary is such a movement of the side-walls or floor of the chest, or of both, that the capacity of the interior shall be enlarged. By such increase of capacity there will be of course a diminution of the pressure of the air in the lungs, and a fresh quantity will enter through the larynx and trachea to equalise the pressure on the inside and outside of the chest. For the *expiration* of air, on the other hand, it is also evident, that, by an opposite movement which shall diminish the capacity of the chest, the pressure in the interior will be increased, and air will be expelled, until the pressures within and without the chest are again equal. In both cases the air passes through the trachea and larynx,

whether in entering or leaving the lungs, there being no other communication with the exterior of the body; and the lung, for the reason before mentioned, remains under all the circumstances described, closely in contact with the walls and floor of the chest. To speak of expansion of the chest, is to speak also of expansion of the lung.

We have now to consider the means by which the chest-cavity is alternately enlarged and contracted for the entrance and expulsion of atmospheric air; or, in technical terms, for *inspiration* and *expiration*.

Respiratory Movements.

The enlargement of the chest in *inspiration* is a muscular act; the effect of the action of the inspiratory muscles being an increase in the size of the chest-cavity (*a*) in the vertical, and (*b*) in the lateral and antero-posterior diameters.

(*a*.) The *vertical* diameter of the chest is increased by the contraction and consequent descent of the diaphragm,—the sides of the muscle descending most, and the central tendon remaining comparatively unmoved; while the intercostal, and other muscles, by acting at the same time, prevent the diaphragm, during its contraction, from drawing in the sides of the chest.

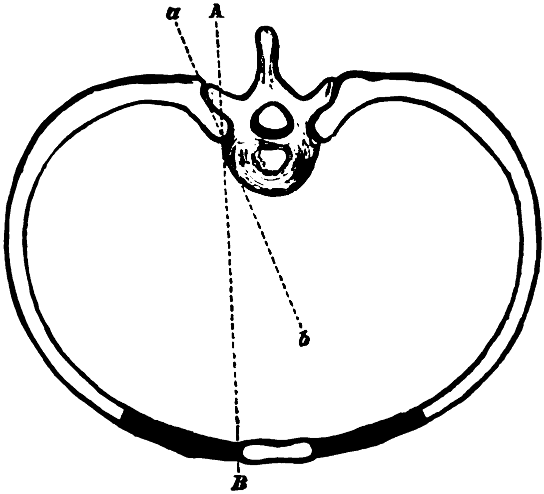
(*b*.) The increase in the lateral and antero-posterior diameters of the chest is effected by the raising of the ribs, the greater number of which are attached very obliquely to the spine and sternum (see Figure of Skeleton in frontispiece).

The elevation of the ribs takes place both in front and at the sides—the hinder ends being prevented from performing any upward movement by their attachment to the spine. The movement of the front extremities of the ribs is of necessity accompanied by an upward and forward movement of the sternum to which they are attached, the movement being greater at the lower than at the upper end of the latter bone.

The axes of rotation in these movements are two; one corresponding with a line drawn through the two articulations which the

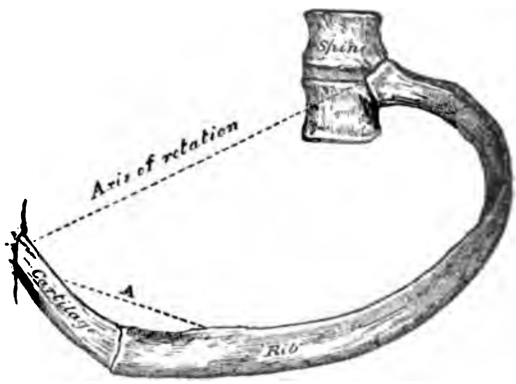
rib forms with the spine (*a b*, fig. 127); and the other, with a line

Fig. 127.



drawn from one of these (head of rib) to the sternum (A B, fig. 127

Fig. 128.



and fig. 128); the motion of the rib around the latter axis being somewhat after the fashion of raising the handle of a bucket.

The elevation of the ribs is accompanied by a slight opening out of the angle which the bony part forms with its cartilage (fig. 128 A); and thus an additional means is provided for increasing the antero-posterior diameter of the chest.

The muscles by which the ribs are raised, in *ordinary* quiet inspiration, are the *external* intercostals, and that portion of the internal intercostals which is situate between the costal cartilages; and these are assisted by the *levatores costarum*, and the *serratus posticus superior*. The action of the last-named muscles is very simple. Their fibres, arising from the spine as a fixed point, pass obliquely downwards and forwards to the ribs, and necessarily raise the latter when they contract. The action of the intercostal muscles is not quite so simple, inasmuch as, passing merely from rib to rib, they seem at first sight to have no fixed point towards which they can pull the bones to which they are attached.

A very simple apparatus, however, will explain this apparent

Fig. 129.*

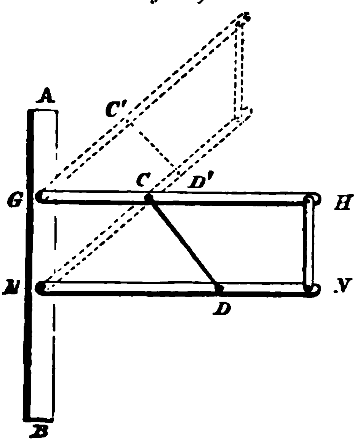
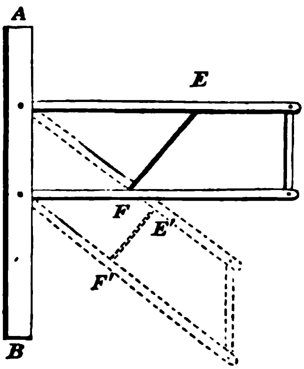


Fig. 130.†



anomaly and make their action plain. Such an apparatus is shown in fig. 129. A B is an upright bar, representing

* Fig. 129. Diagram of apparatus showing the action of the *external* intercostal muscles.

† Fig. 130. Ditto, *internal* intercostal muscles.

the spine, with which are jointed two parallel bars, G H and M N, which represent two of the ribs, and are connected in front by moveable joints with another upright, H N, representing the sternum.

If with such an apparatus elastic bands be connected in imitation of the intercostal muscles, it will be found that when stretched on the bars after the fashion of the *external* intercostal fibres (fig. 129 C D), *i.e.* passing downwards and forwards, they raise them (fig. 129 C′ D′); while, on the other hand, if placed in imitation of the position of the *internal* intercostals (fig. 130 E F), *i.e.*, passing downwards and backwards, they depress them (fig. 130 E′ F′).

The explanation of the foregoing facts is very simple. The intercostal muscles in contracting, merely do that which all other contracting fibres do, viz., bring nearer together the points to which they are attached; and in order to do this, the *external* intercostals must raise the ribs, the points C and D (fig. 129) being nearer to each other when the parallel bars are in the position of the dotted lines. The limit of the movement in the apparatus is reached when the elastic band extends at right angles to the two bars which it connects—the points of attachment C′ and D′ being then at the smallest possible distance one from the other.

The *internal* intercostals (excepting those fibres which are attached to the cartilages of the ribs), have an opposite action to that of the external. In contracting they must pull down the ribs, because the points E and F (fig. 130) can only be brought nearer one to another (fig. 130 E′ F′) by such an alteration in their position.

On account of the oblique position of the *cartilages* of the ribs with reference to the sternum (see Figure of Skeleton in frontispiece), the action of the *inter-cartilaginous* fibres of the internal intercostals must, of course, on the foregoing principles, resemble that of the external intercostals.

In tranquil breathing, the expansive movements of the lower part of the chest are greater than those of the upper. In forced inspiration, on the other hand, according to Dr. A. Ransome, the

greatest extent of movement appears to be in the upper antero-posterior diameter.

In *extraordinary* or forced inspiration, as in violent exercise, or in cases in which there is some interference with the due entrance of air into the chest, and in which, therefore, strong efforts are necessary, other muscles than those just enumerated are pressed into the service. It is very difficult or impossible to separate by a hard and fast line, the so-called muscles of *ordinary* from those of *extraordinary* inspiration; but there is no doubt that the following are but little used *as respiratory agents*, except in cases in which unusual efforts are required—the *scalene* muscles, the *sternomastoid*, the *serratus magnus*, the *pectorales*, and the *trapezius*.

The expansion of the chest in inspiration presents some peculiarities in different persons. In young children, it is effected chiefly by the diaphragm, which being highly arched in expiration, becomes flatter as it contracts, and, descending, presses on the abdominal viscera, and pushes forward the front walls of the abdomen. The movement of the abdominal walls being here more manifest than that of any other part, it is usual to call this the *abdominal* type of respiration. In adults, together with the descent of the diaphragm, and the pushing forward of the front wall of the abdomen, the chest and the sternum are subject to a wide movement in inspiration. In women, the movement appears less extensive in the lower, and more so in the upper, part of the chest—*costal* type.

From the enlargement produced in inspiration, the chest and lungs return in ordinary tranquil expiration, by their elasticity; the force employed by the inspiratory muscles in distending the chest and overcoming the elastic resistance of the lungs and chest-walls, being returned as an expiratory effort when the muscles are relaxed. This elastic recoil of the lungs is sufficient, in ordinary quiet breathing, to expel air from the chest in the intervals of inspiration, and no muscular power is required. In all voluntary expiratory efforts, however, as in speaking, singing, blowing, and the like, and in many involuntary actions also, as sneezing, coughing, etc., something more than merely

passive elastic power is necessary, and the proper expiratory muscles are brought into action. By far the chief of these

Fig. 131.*

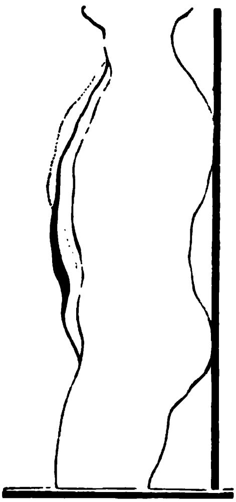
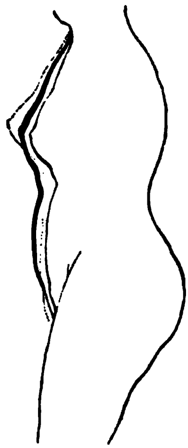


Fig. 132.†



are the abdominal muscles, which, by pressing on the viscera of the abdomen, push up the floor of the chest formed by the diaphragm, and by thus making pressure on the lungs, expel air from them through the trachea and larynx. All muscles, however, which depress the ribs, must act also as muscles of

* Fig. 131 (after Hutchinson). The changes of the thoracic and abdominal walls of the male during respiration. The back is supposed to be fixed in order to throw forward the respiratory movement as much as possible. The outer black continuous line in front represents the ordinary breathing movement: the anterior margin of it being the boundary of inspiration, the posterior margin the limit of expiration. The line is thicker over the abdomen, since the ordinary respiratory movement is chiefly abdominal: thin over the chest, for there is less movement over that region. The dotted line indicates the movement on deep inspiration, during which the sternum advances while the abdomen recedes.

† Fig. 132 (after Hutchinson). The respiratory movement in the female. The lines indicate the same changes as in the last figure. The thickness of the continuous line over the sternum shows the larger extent of the ordinary breathing movement over that region in the female than in the male.

expiration, and therefore we must conclude that the abdominal muscles are assisted in their action by the greater part of the *internal* inter-costals, the *triangularis sterni*, the *serratus posticus inferior*, and *quadratus lumborum*. When by the efforts of the expiratory muscles, the chest has been squeezed to less than its average diameter, it again, on relaxation of the muscles, returns to the normal dimensions by virtue of its elasticity. The construction of the chest-walls, therefore, admirably adapts them for recoiling against and resisting as well undue contraction as undue dilatation.

As before mentioned, the lungs, after distension in the act of inspiration, contract by virtue of the elastic tissue which is present in the bronchial tubes, on and between the air-cells, and in the investing pleura. But in the natural condition of the parts, they can never contract to the utmost, but are always more or less "on the stretch," being kept closely in contact with the inner surface of the walls of the chest by atmospheric pressure (p. 228) and can contract away from these only when, by some means or other, as by making an opening into the pleural cavity, or by the effusion of fluid there, the pressure on the exterior and interior of the lungs becomes equal. Thus, under ordinary circumstances, the degree of contraction or dilatation of the lungs is dependent on that of the boundary walls of the chest, the outer surface of the one being in close contact with the inner surface of the other, and obliged to follow it in all its movements.

Respiratory Rhythm.

The acts of expansion and contraction of the chest, take up, under ordinary circumstances, a nearly equal time. The act of inspiring air, however, especially in women and children, is a little shorter than that of expelling it, and there is commonly a very slight pause between the end of expiration and the beginning of the next inspiration. The respiratory rhythm may be thus expressed:—

Inspiration	6
Expiration	7 or 8

A very slight pause.

Respiratory Sounds.

If the ear be placed in contact with the wall of the chest, or be separated from it only by a good conductor of sound, a faint *respiratory murmur* is heard during both inspiration and expiration—the former being the most audible. This sound, which is produced by the friction of the air as it streams into or out of the lungs, against the inner surface of the bronchial tubes and air-cells, varies somewhat in different parts—being loudest or coarsest in the neighbourhood of the trachea and large bronchi, and fading off into a faint sighing as the ear is placed at a distance from these. It is best heard in children.

Respiratory Movements of the Glottis

During the action of the muscles which directly draw air into the chest, those which guard the opening through which it enters are not passive. In hurried breathing the instinctive dilatation of the nostrils is well seen, although under ordinary conditions it may not be noticeable. The opening at the upper part of the larynx, however, or *rima glottidis* (fig. 133), is dilated at each inspiration, for the more ready passage of air, and collapses somewhat at each expiration; its condition, therefore, corresponding during respiration with that of the walls of the chest. There is a further likeness between the two acts in that, under ordinary circumstances, the dilatation of the rima glottidis is a muscular act, and its contraction chiefly an elastic recoil; although, under various conditions, to be hereafter mentioned, there may be, in the contraction of the glottis, considerable muscular power exercised.

The movements of the glottis are regulated by the laryngeal branches of the vagus, of which the superior is the afferent (sensory) nerve, and the inferior or recurrent nerve the efferent (motor) nerve. The superior laryngeal nerve appears to be one channel through which the general respiratory movements are slackened. When it is cut across, and the proximal end stimulated, the inspirations are diminished in frequency, while if the stimulus be increased, the diaphragm stands still, and the expiratory muscles are thrown into activity (Rosenthal).

Quantity of Air Respired.

The average quantity of air that is changed in the lungs in each act of ordinary tranquil breathing is, in healthy young and middle-aged men, about 30 to 35 cubic inches. In the female, the amount is somewhat less.

The total quantity of air which passes into and out of the lungs of an adult, at rest, in 24 hours, is about 686,000 cubic inches (E. Smith). This quantity, however, is largely increased by exertion; and the same observer has computed the average amount for a hard-working labourer in the same time, at 1,568,390 cubic inches.

The quantity which is habitually and almost uniformly changed in each act of breathing, is called by Mr. Hutchinson *breathing air*. The quantity over and above this which can be drawn into the lungs in the deepest inspiration, he names *complemental air:* its amount is various, as will be presently shown. After ordinary expiration, such as that which expels the *breathing* or *tidal air*, a certain quantity of air remains in the lungs, which may be expelled by a forcible and deeper expiration: this is termed *reserve* or *supplemental air*. But, even after the most violent expiratory effort, the lungs are not completely emptied; a certain quantity always remains in them, over which there is no voluntary control, and which may be called *residual air*. Its amount depends in great measure on the absolute size of the chest, but may be estimated at about a hundred cubic inches (Hutchinson).

The greatest respiratory capacity of the chest is indicated by the quantity of air which a person can expel from his lungs by a forcible expiration after the deepest inspiration that he can make. Mr. Hutchinson names this the *vital capacity;* it expresses the power which a person has of breathing in the emergencies of active exercise, violence, and disease.

The *vital*, or, as it may be better termed, the *respiratory* capacity, is usually measured by a modified gasometer (*spirometer* of Hutchinson), into which the experimenter breathes,—making the most prolonged expiration possible after the deepest possible inspiration. The quantity of air which is thus expelled from the lungs is indicated by the height to which the air-

chamber of the spirometer rises; and by means of a scale placed in connection with this, the number of cubic inches is read off.

In healthy men, the respiratory capacity varies chiefly with the stature, weight, and age.

It was found by Mr. Hutchinson, from whom most of our information on this subject is derived, that at a temperature of 60° F., 225 cubic inches is the average *vital* or respiratory *capacity* of a healthy person, five feet seven inches in height. For every inch of height above this standard the capacity is increased, on an average, by eight cubic inches; and for every inch below, it is diminished by the same amount. This relation of capacity to height is quite independent of the absolute capacity of the cavity of the chest; for the cubic contents of the chest do not always, or even generally, increase with the stature of the body; and a person of small absolute capacity of chest may have a large capacity of respiration, and *vice versâ*. The capacity of respiration is determined only by the mobility of the walls of the chest; but why this mobility should increase in a definite ratio with the height of the body is yet unexplained, and must be difficult of solution, seeing that the height of the body is chiefly determined by that of the legs, and not by the height of the trunk or the depth of the chest. But the vast number of observations made by Mr. Hutchinson seem to leave no doubt of the fact as stated above.

The influence of *weight* on the capacity of respiration is less manifest and considerable than that of height: and it is difficult to arrive at any definite conclusions on this point, because the natural average weight of a healthy man in relation to stature has not yet been determined. As a general statement, however, it may be said that the capacity of respiration is not affected by weights under 161 pounds, or 11½ stones; but that, above this point, it is diminished at the rate of one cubic inch for every additional pound up to 196 pounds, or 14 stones; so that, for example, while a man of five feet six inches, and weighing less than 11½ stones, should be able to expire 217 cubic inches, one of the same height, weighing 12½ stones, might expire only 203 cubic inches.

By *age*, the capacity appears to be increased from about the fifteenth to the thirty-fifth year, at the rate of five cubic inches per year; from thirty-five to sixty-five it diminishes at the rate of about one and a-half cubic inch per year; so that the capacity of respiration of a man of sixty years old would be about 30 cubic inches less than that of a man forty years old, of the same height and weight.

The *number* of respirations in a healthy adult person usually ranges from fourteen to eighteen per minute. It is greater in infancy and childhood. It varies also much according to different circumstances, such as exercise or rest, health or disease, etc. Variations in the number of respirations correspond ordinarily with similar variations in the pulsations of the heart.

In health the proportion is about 1 to 4, or 1 to 5, and when the rapidity of the heart's action is increased, that of the chest movement is commonly increased also; but not in every case in equal proportion. It happens occasionally in disease, especially of the lungs or air-passages, that the number of respiratory acts increases in quicker proportion than the beats of the pulse; and, in other affections, much more commonly, that the number of the pulses is greater in proportion than that of the respirations.

There can be no doubt that the number of respirations of any given animal is largely affected by its size. Thus, comparing animals of the same kind, in a tiger (lying quietly) the number of respirations was 20 per minute, while in a small leopard (lying quietly) the number was 30. In a small monkey, 40 per minute; in a large baboon, 20.

The rapid, panting respiration of mice, even when quite still, is familiar, and contrasts strongly with the slow breathing of a large animal such as the elephant (eight or nine times per minute). These facts may be explained as follows:—The heat-producing power of any given animal depends largely on its bulk, while its loss of heat depends to a great extent upon the surface area of its body. If of two animals of similar shape, one be ten times as long as the other, the area of the large animal (representing its loss of heat) is 100 times that of the small one, while its bulk (representing production of heat) is 1000 times as great. Thus, in order to balance its much greater relative loss of heat, the smaller animal must have all its vital functions, circulation, respiration, &c., carried on much more rapidly.

According to Mr. Hutchinson, the *force* with which the inspiratory muscles are capable of acting, is greatest in individuals of the height of from five feet seven inches to five feet eight inches, and will elevate a column of three inches of mercury. Above this height, the force decreases as the stature increases; so that the average of men of six feet can elevate only about two and a half inches of mercury. The force manifested in the strongest expiratory acts is, on the average, one-third greater than that exercised in inspiration. But this difference is in great measure due to the power exerted by the elastic reaction of the walls of the chest; and it is also much influenced by the disproportionate strength which the expiratory muscles attain, from their being called into use for other purposes than that of simple expiration. The force of the inspiratory act is, therefore, better adapted than that of the expiratory for testing the muscular strength of the body.

The following Table expresses the result of numerous experiments by Mr. Hutchinson on this subject, the instrument used to gauge the inspiratory and expiratory power being a mercurial manometer, to which was attached a tube fitting the nostrils, and through which the inspiratory or expiratory effort was made :—

Power of Inspiratory Muscles.		Power of Expiratory Muscles.
1·5 in.	Weak	2·0 in.
2·0 ,,	Ordinary	2·5 ,,
2·5 ,,	Strong	3·5 ,,
3·5 ,,	Very strong	4·5 ,,
4·5 ,,	Remarkable	5·8 ,,
5·5 ,,	Very remarkable	7·0 ,,
6·0 ,,	Extraordinary	8·5 ,,
7·0 ,,	Very extraordinary	10·0 ,,

The great force of the inspiratory efforts during apnœa was well shown in some of the experiments performed by the Medico-Chirurgical Society's Committee on Suspended Animation. On inserting a glass tube into the trachea of a dog, and immersing the other end of the tube in a vessel of mercury, the respiratory efforts during apnœa were so great as to draw the mercury four inches up the tube. The influence of the same force was shown in other experiments, in which the heads of animals were immersed both in mercury and in liquid plaster of Paris. In both cases the material was found, after death, to have been drawn up into all the bronchial tubes, filling the tissue of the lungs.

The greater part of the force exerted in deep inspiration is employed in overcoming the resistance offered by the elasticity of the walls of the chest and of the lungs.

Mr. Hutchinson estimated the amount of this elastic resistance, by observing the elevation of a column of mercury raised by the return of air forced, after death, into the lungs, in quantity equal to the known capacity of respiration during life; and he calculated, according to the well-known hydrostatic law of equality of pressures (as shown in the Bramah press), that the total force to be overcome by the muscles in the act of inspiring 200 cubic inches of air is more than 450 lbs.

The elastic force overcome in ordinary inspiration is, according to Hutchinson, equal to about 170 pounds.

Dr. Douglas Powell has recently shown that within the limits of *ordinary tranquil respiration*, the elastic resilience of the *walls of the chest* favours *inspiration;* and that it is only in deep

inspiration that the ribs and rib-cartilages offer an opposing force to their dilatation. In other words, the elastic resilience of the lungs, at the end of an act of ordinary breathing, has drawn the chest-walls within the limits of their normal degree of expansion.

Under all circumstances, of course, the elastic tissue of the *lungs* opposes inspiration, and favours expiration.

It is probable, that in the quiet ordinary respiration, which is performed without consciousness or effort of the will, the only forces engaged are those of the inspiratory muscles, and the elasticity of the walls of the chest and the lungs.

It is possible, as Dr. R. Hall maintained, that the contractile power which the bronchial tubes possess, by means of their organic muscular fibres may (1) assist in expiration; but it is more likely that its chief purpose is (2) to regulate and adapt, in some measure, the quantity of air admitted to the lungs, and to each part of them, according to the supply of blood.

Another purpose served by the muscular fibres of the bronchial tubes is (3) that of contracting upon and gradually expelling collections of mucus, which may have accumulated within the tubes, and cannot be ejected by forced expiratory efforts, owing to collapse or other morbid conditions of the portion of lung connected with the obstructed tubes (Gairdner).

The muscular action in the lungs, morbidly excited, is probably the chief cause of the phenomena of spasmodic asthma. It may be demonstrated by galvanising the lungs shortly after taking them from the body. Under such a stimulus, they contract so as to lift up water placed in a tube introduced into the trachea (C. J. B. Williams); and Volkmann has shown that they may be made to contract by stimulating their nerves. He tied a glass tube, drawn fine at one end, into the trachea of a beheaded animal; and when the small end was turned to the flame of a candle, he galvanised the pneumogastric trunk. Each time he did so the flame was blown, and once it was blown out.

The changes of the air in the lungs effected by the respiratory movements are assisted by the various conditions of the air

itself. According to the law observed in the diffusion of gases, the carbonic acid evolved in the air-cells will, independently of any respiratory movement, tend to leave the lungs, by diffusing itself into the external air, where it exists in less proportion; and according to the same law, the oxygen of the atmospheric air will tend of itself towards the air-cells in which its proportion is less than it is in the air in the bronchial tubes or in that external to the body. But for this tendency in the oxygen and carbonic acid to mix uniformly, within and without the lungs, the *reserve* and *residual* air would be very injuriously charged with carbonic acid; for the respiratory movements alone are not enough to empty the air cells; and they, perhaps, expel only the air which lies in the larger bronchial tubes. The change is also assisted by the different temperature of the air within and without the lungs; and by the action of the cilia on the mucous membrane of the bronchial tubes, the continual vibrations of which may serve to prevent the adhesion of the air to the moist surface of the membrane.

Daily Work of the Respiratory Muscles.

According to Dr. Haughton the work done by the respiratory muscles in 24 hours amounts to 21 foot-tons.

Circulation of Blood in the Respiratory Organs.

To be exposed to the air thus alternately moved into and out of the air-cells and minute bronchial tubes, the blood is propelled from the right ventricle through the pulmonary capillaries in steady streams, and slowly enough to permit every minute portion of it to be for a few seconds exposed to the air, with only the thin walls of the capillary vessels and air-cells intervening. The pulmonary circulation is of the simplest kind: for the pulmonary artery branches regularly; its successive branches run in straight lines, and do not anastomose; the capillary plexus is uniformly spread over the air-cells and intercellular passages; and the veins derived from it proceed in a course as simple and uniform as that of the arteries, their branches

converging but not anastomosing. The veins have no valves, or only small imperfect ones prolonged from their angles of junction, and incapable of closing the orifice of either of the veins between which they are placed. The pulmonary circulation also is unaffected by changes of atmospheric pressure, and is not exposed to the influence of the pressure of muscles: the force by which it is accomplished, and the course of the blood are alike simple.

The blood which is conveyed to the lungs by the *pulmonary* arteries is distributed to these organs to be purified and made fit for the nutrition of all other parts of the body. The capillaries of the pulmonary vessels are arranged solely with reference to this object, and therefore can have but little to do with the *nutrition* of the lungs; or at least, only of those portions of the lungs with which they are in intimate connection for another purpose. For the nutrition of the rest of the lungs, including the pleura, interlobular tissue, bronchial tubes and glands, and the walls of the larger blood-vessels, a special supply of arterial blood is furnished through one or two *bronchial* arteries, the branches of which ramify in all these parts. The blood of the bronchial artery, when, having served for the nutrition of these parts, it has become venous, is carried partly into the branches of the bronchial vein, and thence to the *right* auricle, and partly into the small branches of the pulmonary artery, or, more directly, into the pulmonary capillaries, whence, being with the rest of the blood arterialised, it is carried to the pulmonary veins and *left* side of the heart.

Changes of the Air in Respiration.

By their contact in the lungs the composition of both air and blood is changed. The alterations of the former being manifest, simpler than those of the latter, and in some degree illustrative of them, may be considered first.

The *atmosphere* we breathe has, in every situation in which it has been examined in its natural state, a nearly uniform composition. It is a mixture of oxygen, nitrogen, carbonic acid, and watery vapour, with, commonly, traces of other gases, as ammonia, sulphuretted hydrogen, etc. Of every

100 volumes of pure atmospheric air, 79 volumes (on an average) consist of nitrogen, the remaining 21 of oxygen. The proportion of carbonic acid is extremely small; 10,000 volumes of atmospheric air contain only about 4 or 5 of carbonic acid.

The quantity of watery vapour varies greatly, according to the temperature and other circumstances, but the atmosphere is never without some. In this country, the average quantity of watery vapour in the atmosphere is 1·40 per cent.

The changes produced by respiration on the atmospheric air are, that, 1, it is warmed; 2, its carbonic acid is increased; 3, its oxygen is diminished; 4, its watery vapour is increased; 5, a minute amount of organic matter and of free ammonia is added to it.

1. The expired air, heated by its contact with the interior of the lungs, is (at least in most climates) hotter than the inspired air. Its temperature varies between 97° and 99½°, the lower temperature being observed when the air has remained but a short time in the lungs, rather than when it is inhaled at a very low temperature; for whatever the temperature when inhaled may be, the air nearly acquires that of the blood before it is expelled from the chest.

2. *The carbonic acid in respired air is always increased;* but the quantity exhaled in a given time is subject to change from various circumstances. From every volume of air inspired, about 4½ per cent. of oxygen is abstracted; while a rather smaller quantity of carbonic acid is added in its place. Under ordinary circumstances, the quantity of carbonic acid exhaled into the air breathed by a healthy adult man amounts to 1346 cubic inches, or about 636 grains per hour. (Valentin and Brunner.) According to this estimate, the weight of carbon excreted from the lungs is about 173 grains per hour, or rather more than 8 ounces in twenty-four hours. These quantities must be considered approximate only, inasmuch as various circumstances even in health, influence the amount of carbonic acid excreted, and, correlatively, the amount of oxygen absorbed. The following are the chief:—Age and sex. Respiratory movements. External temperature. Season of year. Condition of respired air. Atmospheric conditions. Period of the day. Food and drink. Exercise and sleep.

a. Age and Sex.—According to Andral and Gavarret the quantity of carbonic acid exhaled into the air breathed by males, regularly increases from eight to thirty years of age; from thirty to forty it is stationary or diminishes a little; from forty to fifty the diminution is greater; and from fifty to extreme age it goes on diminishing, till it scarcely exceeds the quantity exhaled at ten years old. In females (in whom the quantity exhaled is always less than in males of the same age) the same regular increase in quantity goes on from the eighth year to the age of puberty, when the quantity abruptly ceases to increase, and remains stationary so long as they continue to menstruate. When, however, menstruation has ceased, either in advancing years or in pregnancy, or morbid amenorrhœa, the exhalation of carbonic acid again augments; but when menstruation ceases naturally, it soon decreases again at the same rate that it does in old men.

b. Respiratory Movements.—According to Vierordt, the more quickly the movements of respiration are performed, the smaller is the proportionate quantity of carbonic acid contained in each volume of the expired air. Thus he found that, with six respirations per minute, the quantity of expired carbonic acid was 5·528 per cent.; with twelve respirations, 4·262 per cent.; with twenty-four, 3·355; with forty-eight, 2·984; and with ninety-six, 2·662. Although, however, the proportionate quantity of carbonic acid is thus diminished during frequent respiration, yet the absolute amount exhaled into the air within a given time is increased thereby, owing to the larger quantity of air which is breathed in the time. This is the case, whether the respiration be voluntarily accelerated, or naturally increased in frequency, as it is after feeding, active exercise, etc. By diminishing the frequency, and increasing the depth of respiration, the per-centage proportion of carbonic acid in the expired air is diminished; being in the deepest respiration as much as 1·97 per cent. less than in ordinary breathing. But for this proportionate diminution also, there is a full compensation in the greater total volume of air which is thus breathed. Finally, the last half of a volume of expired air contains more carbonic acid than the half first expired; a circumstance which is explained by the one portion of air coming from the remote part of the lungs, where it has been in more immediate and prolonged contact with the blood than the other has, which comes chiefly from the larger bronchial tubes.

c. External Temperature.—The observations made by Vierordt at various temperatures between 38° F. and 75° F. show, for warm-blooded animals, that within this range, every rise equal to 10° F. causes a diminution of about two cubic inches in the quantity of carbonic acid exhaled per minute. Letellier, from experiments performed on animals at much higher and lower temperatures than the above, also found that the higher the temperature of the respired air (as far as 104° F.), the less is the amount of carbonic acid exhaled into it, whilst the nearer it approaches zero the more does the carbonic acid increase.

d. Season of the Year.—The season of the year, independently of temperature, materially influences the respiratory phenomena; spring being the season of the greatest, and autumn of the least activity of the respiratory and other functions. (Edward Smith.)

e. Purity of the Respired Air.—The average quantity of carbonic acid given out by the lungs constitutes about 4·48 per cent. of the expired air;

but if the air which is breathed be previously impregnated with carbonic acid (as is the case when the same air is frequently respired), then the quantity of carbonic acid exhaled becomes much less. This is shown by the results of two experiments performed by Allen and Pepys. In one, in which fresh air was taken in at each respiration, thirty-two cubic inches of carbonic acid were exhaled in a minute; whilst in the other, in which the same air was respired repeatedly, the quantity of carbonic acid emitted in the same time was only 9·5 cubic inches. They found also that, however often the same air may be respired, even if until it will no longer sustain life, it does not become charged with more than ten per cent. of carbonic acid.

In the normal process of respiration, the elimination of carbonic acid by the lungs appears to depend on the fact that its *tension* in the venous blood circulating in the lung far exceeds that of the carbonic acid in the inspired air. Carbonic acid will therefore be eliminated as long as its tension in the inspired air is less than in the blood; as soon as they become equalized (as by breathing the same air again and again, which will of course increase the quantity, and therefore the tension of carbonic acid in the respired air), no further elimination can occur.

f. Hygrometric State of Atmosphere.—The amount of carbonic acid exhaled is considerably influenced by the degree of moisture of the atmosphere, much more being given off when the air is moist than when it is dry. (Lehmann.)

g. Period of the Day.—During the day-time more carbonic acid is exhaled than corresponds to the oxygen absorbed; while, on the other hand, at night very much more oxygen is absorbed than is exhaled in carbonic acid. There is, thus, a *reserve fund* of oxygen absorbed by night, to meet the requirements of the day.

If the total quantity of carbonic acid exhaled in 24 hours be represented by 100, 52 parts are exhaled during the day and 48 at night. While, similarly, 33 parts of the oxygen are absorbed during the day, and the remaining 67 by night. (Pettenkofer and Voit.)

The *period of day* seems to exercise a slight influence on the amount of carbonic acid exhaled in a given time, though beyond the fact that the quantity exhaled is much less by night, we are scarcely in a position to state that variations in the amount exhaled occur at uniform periods of the day, independently of the influence of other circumstances.

h. Food and Drink.—By the use of *food* the quantity is increased, whilst by fasting it is diminished: and, according to Regnault and Reiset, it is greater when animals are fed on farinaceous food than when fed on meat. Dr. Edward Smith found that the effects produced by spirituous drinks depend much on the kind of drink taken. Pure alcohol tended rather to increase than to lessen respiratory changes, and the amount therefore of carbonic acid expired: rum, ale and porter, also sherry, had very similar effects. On the other hand, brandy, whisky and gin, particularly the latter, almost always lessened the respiratory changes, and consequently the amount of carbonic acid exhaled.

i. Exercise and Sleep.—*Bodily exercise*, in moderation, increases the quantity to about one-third more than it is during rest: and for about an hour after exercise, the volume of the air expired in the minute is increased

about 118 cubic inches: and the quantity of carbonic acid about 7·8 cubic inches per minute. Violent exercise, such as full labour on the treadwheel, still further increases the amount of the acid exhaled. (Edward Smith.)

During *sleep*, on the other hand, there is a considerable diminution in the quantity of this gas evolved; a result probably in great measure dependent on the tranquillity of breathing.

A larger quantity is exhaled when the barometer is low than when it is high.

3. *The Oxygen in Respired Air is always less* than in the same air before respiration, and its diminution is generally proportionate to the increase of the carbonic acid.

The absorption of *oxygen* from inspired air would appear to depend not so much on a difference of tension of the gas in the air and venous blood, as on the strong chemical affinity which hæmoglobin has for it (p. 117). Since the oxygen enters into chemical combination with the hæmoglobin, its tension in the blood is very small, and hence an animal breathing in a closed space will consume almost all the oxygen in the contained air, though its tension constantly diminishes, if provision be made for the constant removal of the carbonic acid.

For every volume of carbonic acid exhaled into the air, 1·17421 volumes of oxygen are absorbed from it: and when the average quantity of carbonic acid, *i.e.*, 1346 cubic inches, or 636 grains, is exhaled in the hour, the quantity of oxygen absorbed in the same time is 1584 cubic inches or 542 grains (Valentin and Brunner). According to this estimate, there is more oxygen absorbed than is exhaled with carbon to form carbonic acid without change of volume; and to this general conclusion, namely, that the volume of air expired in a given time is less than that of the air inspired (allowance being made for the expansion in being heated), and that the loss is due to a portion of oxygen absorbed and not returned in the exhaled carbonic acid, all observers agree, though as to the actual quantity of oxygen so absorbed, they differ even widely.

The quantity of oxygen that does not combine with the carbon given off in carbonic acid from the lungs, is probably disposed of in forming some of the carbonic acid and water given off from the skin, and in combining with sulphur and phosphorus to form part of the acids of the sulphates and phosphates excreted in the urine, and probably also, from the experiments of Dr. Bence Jones, with the nitrogen of the decomposing nitrogenous tissues.

The quantity of oxygen in the atmosphere surrounding

animals, appears to have very little influence on the amount of this gas absorbed by them, for the quantity consumed is not greater even though an excess of oxygen be added to the atmosphere experimented with (Regnault and Reiset).

The Nitrogen of the Atmosphere, in relation to the respiratory process, is supposed to serve only mechanically, by diluting the oxygen, and moderating its action upon the system.

This purpose, or the mode of expressing it, has been denied by Liebig, on the ground that if we suppose the nitrogen removed, the amount of oxygen in a given space would not be altered. But, although it be true that, if all the nitrogen of the atmosphere were removed and not replaced by any other gas, the oxygen might still extend over the whole space at present occupied by the mixture of which the atmosphere is composed; yet since, under ordinary circumstances, oxygen and nitrogen, when mixed together in the ratio of one volume to four, produce a mixture which occupies precisely five volumes, with all the properties of atmospheric air, it must result that a given volume of atmosphere drawn into the lungs contains four-fifths less weight of oxygen than an equal volume composed entirely of oxygen. The greater rapidity and brilliancy with which combustion goes on in an atmosphere of oxygen than in one of common air, and the increased rapidity with which the ordinary effects of respiration are produced when oxygen instead of atmospheric air is breathed, leave no doubt that the nitrogen with which the oxygen of the atmosphere is mixed, has the effect of diluting this gas, under the present conditions of atmospheric pressure, in the same sense and degree as one part of alcohol is diluted when mixed with four parts of water.

It has been often discussed whether nitrogen is absorbed by or exhaled from the lungs during respiration.

At present, all that can be said on the subject is that, under most circumstances, animals appear to expire a very small quantity above that which exists in the inspired air. During prolonged fasting, on the contrary, a small quantity appears to be absorbed.

4. *Watery Vapour* is, under ordinary circumstances, always exhaled from the lungs in breathing. The quantity emitted is, as a general rule, sufficient to saturate the expired air, or very nearly so. Its absolute amount is, therefore, influenced by the following circumstances, (1), by the quantity of air respired; for the greater this is, the greater also will be the quantity of moisture exhaled. (2), by the quantity of watery vapour contained in the air previous to its being inspired; because the

greater this is, the less will be the amount required to complete the saturation of the air; (3) by the temperature of the expired air; for the higher this is, the greater will be the quantity of watery vapour required to saturate the air; (4), by the length of time which each volume of inspired air is allowed to remain in the lungs; for although, during ordinary respiration, the expired air is always saturated with watery vapour, yet when respiration is performed very rapidly the air has scarcely time to be raised to the highest temperature, or be fully charged with moisture ere it is expelled.

The quantity of water exhaled from the lungs in twenty-four hours ranges (according to the various modifying circumstances already mentioned) from about 6 to 27 ounces, the ordinary quantity being about 9 or 10 ounces. Some of this is probably formed by the combination of the excess of oxygen absorbed in the lungs with the hydrogen of the blood; but the far larger proportion of it is water which has been absorbed, as such, into the blood from the alimentary canal, and which is exhaled from the surfaces of the air-passages and cells, as it is from the free surfaces of all moist animal membranes, particularly at the high temperature of warm-blooded animals.

5. The Rev. J. B. Reade showed, some years ago, and Dr. Richardson's experiments confirm the fact, that ammonia is among the ordinary constituents of expired air. It seems probable, however, both from the fact that this substance cannot be always detected, and from its minute amount when present, that the whole of it may be derived from decomposing particles of food left in the mouth, or from carious teeth or the like; and that it is, therefore, only an accidental constituent of expired air.

The quantity of *organic* matter in the breath has been investigated by Dr. A. Ransome, who calculates that about 3 grains are given off from the lungs of an adult in twenty-four hours.

The following represents the kind of experiment by which the foregoing facts regarding the excretion of carbonic acid, water, and organic matter, have been established.

A bird or mouse is placed in a large bottle, through the stopper of which two tubes pass, one to supply fresh air, and the other to carry off that which

has been expired. Before entering the bottle, the air is made to bubble through a strong solution of caustic potash, which absorbs the carbonic acid, and then through lime-water, which by remaining limpid, proves the absence of carbonic acid. The air which has been breathed by the animal is made to bubble through lime-water, which at once becomes turbid, and soon quite milky from the precipitation of calcium carbonate; and it finally passes through strong sulphuric acid, which, by turning brown, indicates the presence of organic matter. The watery vapour in the expired air will condense inside the bottle if the surface be kept cool.

By means of an apparatus, sufficiently large and well constructed, experiments of the kind have been made extensively on man.

Changes produced in the Blood by Respiration.

The most obvious change which the blood of the pulmonary artery undergoes in its passage through the lungs is that of *colour*, the dark crimson of venous blood being exchanged for the bright scarlet of arterial blood. (The circumstances which give rise to this change, and some other differences between arterial and venous blood, were discussed in the chapter on BLOOD, pp. 123–5):—*2nd*, and in connection with the preceding change, it gains oxygen; *3rd*, it loses carbonic acid; *4th*, it becomes 1° or 2° F. warmer; *5th*, it coagulates sooner and more firmly, and, apparently, contains more fibrin.

The oxygen absorbed into the blood from the atmospheric air in the lungs is combined chemically with the hæmoglobin of the red blood-corpuscles. In this condition it is carried in the arterial blood to the various parts of the body, and with it is, in the capillary system of vessels, brought into near relation or contact with the elementary parts of the tissues. In these tissues, and in the blood which circulates in them, a certain portion of the oxygen, which the arterial blood contains, disappears, and a proportionate quantity of carbonic acid and water is formed.

The venous blood, containing the new-formed carbonic acid, returns to the lungs, where a portion of the carbonic acid is exhaled, and a fresh supply of oxygen is again taken in.

The process of respiration has often been compared to that of combustion. When a candle is burnt in a closed space, oxygen

is abstracted, and the air becomes warmer and loaded with carbonic acid and watery vapour. The same changes take place when an animal is confined in a closed space, and in a short time, if no fresh air be admitted, the candle goes out, and the animal dies. But though the resemblance appears to be so close, it is really only a superficial comparison, for respiration is essentially a process of *exchange*, of *elimination*, and *absorption*, in which oxygen is absorbed, and carbonic acid, watery vapour, and heat are given out.

The process of oxidation, which may fairly be compared to the burning of a candle or the rusting of iron, takes place in the tissues all over the body, and necessarily precedes the elimination of the waste products by the lungs.

The experiments of Claude Bernard prove clearly the difference between respiration and combustion. A candle was placed in an atmosphere composed half of oxygen and half of carbonic acid: it was found to burn brilliantly for some time, owing to the large proportion (50 per cent.) of oxygen present. A bird placed in the same atmosphere dies almost at once, for the great tension of carbonic acid in the atmosphere prevents any elimination of carbonic acid from the animal's lungs. That this is the explanation is proved as follows:—

A candle and a small bird are placed each under a bell-glass containing air. After a certain time, the candle will go out and the bird expire. But if, just before this happens, a strong solution of potash be introduced into each to absorb the carbonic acid, the bird will quickly recover, while the candle will go out just as quickly as if no potash had been introduced. If a small bird be placed in this atmosphere, in which the candle has gone out, it will breathe easily for some time. Such an atmosphere contains 15 per cent. of oxygen (the rest having combined with the carbon and hydrogen of the candle to form carbonic acid and water) and 2 per cent. of carbonic acid (the rest having been absorbed by the potash).

Thus we can make an artificial atmosphere in which a candle will burn while an animal will die, and *vice versâ*. The candle goes out from deficiency of oxygen, the animal expires mainly because of the excess of carbonic acid.

Effects of Vitiated Air.—Ventilation.

We have seen that the air expired from the lungs contains a large proportion of carbonic acid and some organic putrescible matter.

Hence it is obvious that if the same air be breathed again and again, the proportion of carbonic acid and organic matter will constantly increase till fatal results are produced; but long

before this point is reached, uneasy sensations occur, such as headache, languor, and a sense of oppression. It is a remarkable fact that the organism after a time adapts itself to such a vitiated atmosphere, and that a person soon comes to breathe, without felt inconvenience, an atmosphere which, when he first entered it, seemed intolerable.

But such an adaptation can only take place at the expense of a depression of all the vital functions, which must be injurious if long continued or often repeated.

This power of adaptation is well illustrated by the experiments of Claude Bernard. A sparrow is placed under a bell-glass of such a size that it will live for three hours. If now at the end of the second hour (when it could have survived another hour) it be taken out and a fresh healthy sparrow introduced, the latter will perish instantly.

The adaptation above spoken of is a gradual and continuous one: thus a bird which will live one hour in a pint of air will live three hours in two pints; and if two birds of the same species, age, and size, be placed in a quantity of air in which either, separately, would survive three hours, they will not live 1½ hours, but only 1¼ hours.

The effects of a vitiated atmosphere, resulting from overcrowding and bad ventilation, may be well illustrated by the following facts:—"The deaths of new-born infants between the ages of 1 and 15 days, which in the Dublin Lying-in Hospital amounted, in the course of four years, to 2944 out of 7650 births, were suddenly reduced to only 279 deaths during the same period, after a new system of ventilation had been adopted. Thus more than 2500 deaths, or 1 in every 3 births, must be attributed to the bad ventilation."

From what has been said it must be evident that provision for a constant and plentiful supply of fresh air, and the removal of that which is vitiated, is of far greater importance than the actual cubic space per head of occupants.

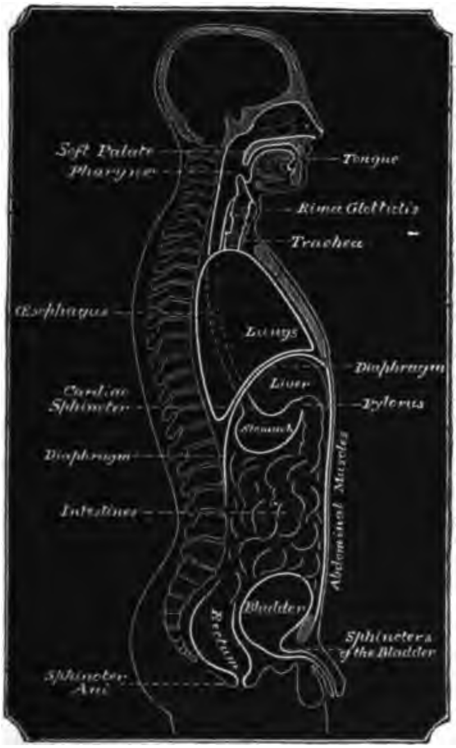
According to Dr. Parkes not less than 2000 cubic feet per head should be allowed in sleeping apartments (barracks, hospitals, &c.), and with this allowance the air can only be maintained at the proper standard of purity by such a system of ventilation as provides for the supply of 1500 to 2000 cubic feet of fresh air per head per hour.

Mechanism of Various Respiratory Actions.

It will be well here, perhaps, to explain some respiratory acts, which appear at first sight somewhat complicated, but cease to

be so when the mechanism by which they are performed is clearly understood. The accompanying diagram (fig. 133) shows that the cavity of the chest is separated from that of the abdomen by the diaphragm, which, when acting, will lessen its curve, and

Fig. 133.



thus descending, will push *downwards and forwards* the abdominal viscera; while the abdominal muscles have the opposite effect, and in acting will push the viscera *upwards and backwards,* and with them the diaphragm, supposing its ascent to be not from any cause interfered with. From the same diagram it will be seen that the lungs communicate with the exterior of the body through the glottis, and further on through the mouth and

nostrils—through either of them separately, or through both at the same time, according to the position of the soft palate. The stomach communicates with the exterior of the body through the œsophagus, pharynx, and mouth; while below, the rectum opens at the anus, and the bladder through the urethra. All these openings, through which the hollow viscera communicate with the exterior of the body, are guarded by muscles, called sphincters, which can act independently of each other. The position of the latter is indicated in the diagram.

Let us take first the simple act of *sighing*. In this case there is a rather prolonged inspiratory effort by the diaphragm and other muscles concerned in inspiration; the air almost noiselessly passing in through the glottis, and by the elastic recoil of the lungs and chest-walls, and probably also of the abdominal walls, being rather suddenly expelled again.

Now, in the first, or *inspiratory* part of this act, the descent of the diaphragm presses the abdominal viscera downwards, and of course this pressure tends to evacuate the contents of such as communicate with the exterior of the body. Inasmuch, however, as their various openings are guarded by sphincter muscles, in a state of constant tonic contraction, there is no escape of their contents, and air simply enters the lungs. In the second, or *expiratory* part of the act of sighing, there is also pressure made on the abdominal viscera in the opposite direction, by the elastic or muscular recoil of the abdominal walls; but the pressure is relieved by the escape of air through the open glottis, and the relaxed diaphragm is pushed up again into its original position. The sphincters of the stomach, rectum, and bladder, act as before.

A familiar illustration of the physiological import of sighing is the well-known fact that when the mind is intensely concentrated on any subject the respirations become very shallow (hence the expression "breathless attention"). This shallow respiration is compensated for by the occurrence of a long sighing inspiration at frequent intervals.

Hiccough resembles sighing in that it is an inspiratory act, but the inspiration is sudden instead of gradual, from the

diaphragm acting suddenly and spasmodically; and the air, therefore, suddenly rushing through the unprepared rima glottidis, causes vibration of the vocal cords, and the peculiar sound.

In the act of *coughing*, there is most often first an inspiration, and this is followed by an expiration; but when the lungs have been filled by the preliminary inspiration, instead of the air being easily let out again through the glottis, the latter is momentarily closed by the approximation of the vocal cords; and then the abdominal muscles, strongly acting, push up the viscera against the diaphragm, and thus make pressure on the air in the lungs until its tension is sufficient to burst open noisily the vocal cords which oppose its outward passage. In this way a considerable force is exercised, and mucus or any other matter that may need expulsion from the lungs or trachea is quickly and sharply expelled by the outstreaming current of air.

Now it is evident on reference to the diagram (fig. 133), that pressure exercised by the abdominal muscles in the act of coughing, acts as forcibly on the abdominal viscera as on the lungs, inasmuch as the viscera form the medium by which the upward pressure on the diaphragm is made, and of necessity there is quite as great a tendency to the expulsion of their contents as of the air in the lungs. The instinctive, and if necessary, voluntarily increased contraction of the sphincters, however, prevents any escape at the openings guarded by them, and the pressure is effective at one part only, namely, the rima glottidis.

The same remarks that apply to coughing, are almost exactly applicable to the act of *sneezing*; but in this instance the blast of air, on escaping from the lungs, is directed by an instinctive contraction of the pillars of the fauces and descent of the soft palate, chiefly through the nose, and any offending matter is thence expelled.

In *speaking*, there is a voluntary expulsion of air through the glottis by means of the abdominal muscles; and the vocal cords are put, by the muscles of the larynx, in a proper position and state of tension for vibrating as the air passes over them, and thus producing sound. The sound is moulded into words by

the tongue, teeth, lips, etc.—the vocal cords producing the sound only, and having nothing to do with *articulation*.

Singing resembles speaking in the manner of its production; the laryngeal muscles, by variously altering the position and degree of tension of the vocal cords, producing the different notes. Words used in the act of singing are of course framed, as in speaking, by the tongue, teeth, lips, etc.

Sniffing is produced by a somewhat quick action of the diaphragm and other inspiratory muscles. The mouth is, however, closed, and by these means the whole stream of air is made to enter by the nostrils. The alæ nasi are, commonly, at the same time, instinctively dilated.

Sucking is not properly a respiratory act, but it may be most conveniently considered in this place. It is caused chiefly by the depressor muscles of the os hyoides. These, by drawing downwards and backwards the tongue and floor of the mouth, produce a partial vacuum in the latter; and the weight of the atmosphere then acting on all sides tends to produce equilibrium on the inside and outside of the mouth as best it may. The communication between the mouth and pharynx is completely shut off, probably by the contraction of the pillars of the soft palate and descent of the latter so as to touch the back of the tongue; and the equilibrium, therefore, can be restored only by the entrance of something through the mouth. The action, indeed, of the tongue and floor of the mouth in sucking may be compared to that of the piston in a syringe, and the muscles which pull down the os hyoides and tongue, to the power which draws the handle.

Sobbing consists in a series of convulsive inspirations, at the moment of which the glottis is usually more or less closed.

Laughing is a series of short and rapid expirations.

Yawning is an act of inspiration, but is unlike most of the preceding actions in being always more or less involuntary. It is attended by a stretching of various muscles about the palate and lower jaw, which is probably analogous to the stretching of the muscles of the limbs in which a weary man finds relief, as a voluntary act, when they have been some time out of action.

The involuntary and reflex character of yawning depends probably on the fact that the muscles concerned are themselves at all times more or less involuntary, and require, therefore, something beyond the exercise of the will to set them in action. For the same reason, yawning, like sneezing, cannot be well performed voluntarily.

In the preceding account of respiratory actions, the diaphragm and abdominal muscles have been, as the chief muscles engaged and for the sake of clearness, almost alone referred to. But, of course, in all *inspiratory* actions, the other muscles of inspiration (p. 233) are also more or less engaged; and in *expiration*, the abdominal muscles are assisted by others, previously enumerated (p. 235) as grouped in action with them.

Influence of the Nervous System in Respiration.

Like all other functions of the body, the discharge of which is necessary to life, respiration must be essentially an involuntary act. Else, life would be in constant danger, and would cease on the loss of consciousness for a few moments, as in sleep. But it is also necessary that respiration should be to some extent under the control of the will. For were it not so, it would be impossible to perform those voluntary respiratory acts which have been just enumerated and explained, as speaking, singing, and the like.

The respiratory movements and their rhythm, so far as they are involuntary and independent of consciousness (as on all ordinary occasions) are under the governance of a nerve-centre in the *medulla oblongata* corresponding with the origin of the pneumogastric nerves; that is to say, the motor nerves and, through them, the muscles concerned in the respiratory movements, are excited by a stimulus which issues from this part of the nervous system. How far the medulla acts *automatically*, *i.e.* how far the stimulus originates in it, or how far it is merely a nerve-centre for *reflex* action, is not certainly known. Probably, both events happen; and, in both cases, the stimulus is the result of the condition of the blood.

On the latter (reflex) theory, the venous blood which the right ventricle propels to the lungs, is the direct excitant of the pneumogastric filaments distributed in these organs; and the stimulus is conveyed by these filaments to the medulla oblongata, and thence *reflected* to the respiratory muscles.

In so far, on the other hand, as the medulla acts automatically, it is by virtue of the condition of the blood which circulates in it. So long as the blood is normal, it is a sufficient stimulus to the sensitive nerve-centre through which it circulates; and rhythmic impulses to respiratory action issue from the medulla. When the relative quantities of carbonic acid and oxygen in the blood are changed, the respiratory movements are changed also. If the oxygen be diminished or the carbonic acid increased, the respiratory movements are proportionally more frequent, and a greater number of muscles are engaged in their performance; while an opposite effect is the result of an excess of oxygen with diminution of carbonic acid.

The *rhythm* of the respiratory movements is best explained in the theory of rhythmic nutrition of the nerve-centres and muscles, as in the case of the heart (p. 166). Of the circumstances which cause the circulatory apparatus to act four or five times as frequently as the respiratory, we know nothing.

Unlike the cardiac rhythm, that of respiration can be for a short time interfered with by the exercise of the will. But the need of breath ("respiratory sense," "besoin de respirer") becomes soon so urgent as to overcome the strongest opposition; and no one has ever committed suicide by simply holding his breath, although, it is said, many have attempted to do so.

The respiratory nerve-centre in the medulla oblongata is very sensitive to impressions other than those which are connected directly or by means of the pulmonary branches of the pneumogastric, with the condition of the blood. The effect on the respiratory movements of the sudden application of cold to the skin (as from a shower bath) and of various mental emotions is well known; and many other examples might be quoted.

At the time of birth, the separation of the placenta, and the consequent non-oxygenation of the fœtal blood, are the circumstances which immediately

lead to the issue of automatic impulses to action from the respiratory centre in the medulla oblongata. But the quickened action which ensues on the application of cold air or water, or other sudden stimulus, to the skin, shows well the intimate connection which exists between this centre and other parts which are not ordinarily connected with the function of respiration.

The dependence of the function of respiration on the medulla oblongata is shown by the cessation of the respiratory movements and, therefore, instant death, which follows an injury to the respiratory nerve-centre, although every other part of the nervous system remain intact. Division of the spinal cord will affect respiration in different degrees according to the place of section. These facts are frequently illustrated by the effects of accidental injury in man. Thus, if the spinal cord be injured in the lower part of the cervical region, inspiration is performed by the diaphragm only, and the chest is almost motionless; because there is an interruption to all communication between the medulla oblongata and the intercostal and many other respiratory muscles. If the injury be somewhat higher in the neck, that is, above the origin of the phrenic nerves, death occurs immediately; the respiratory centre in the medulla being now cut off from the diaphragm also.

In the performance of *voluntary* respiratory acts, the brain, as well as the medulla oblongata, is engaged. But even when the brain is thus in action, it is the medulla oblongata which combines the several respiratory muscles, so that they act harmoniously together; while frequently the same nerve-centre brings into adapted combination of action many other muscles than those commonly exerted in respiration.

Apnœa.—Dyspnœa.—Asphyxia.

As blood which contains a normal proportion of oxygen excites the respiratory *centre* (p. 258), and, as the excitement and consequent respiratory muscular movements are greater (dyspnœa) in proportion to the deficiency of this gas, so an abnormally large proportion of oxygen in the blood leads to diminished breathing movements, and, if large enough, to their temporary cessation. This condition of absence of breathing is termed

*apnœa,** and it can be demonstrated, in one of the lower animals, by performing artificial respiration to the extent of saturating the blood with oxygen.

When, on the other hand, the respiration is stopped, by, *e.g.*, interference with the passage of air to the lungs, or by supplying air devoid of oxygen, a condition ensues, which passes rapidly from the state of *dyspnœa* (difficult breathing) to what is termed *asphyxia;* and the latter quickly ends in death.

The most evident symptoms of asphyxia or suffocation are well-known. Violent action of the respiratory muscles and, more or less, of all the muscles of the body; lividity of the skin and all other vascular parts, while the veins are also distended, and the tissues seem generally gorged with blood; convulsions, quickly followed by insensibility, and death.

The conditions which accompany these symptoms are—

(1) More or less interference with the passage of the blood through the pulmonary blood-vessels.

(2) Accumulation of blood in the right side of the heart and in the systemic veins.

(3) Circulation of impure (non-aërated) blood in all parts of the body.

The causes of these conditions and the manner in which they act, so as to be incompatible with life, may be here briefly considered.

(1) The obstruction to the passage of blood through the lungs is not so great as it was once supposed to be; and such as there is occurs chiefly in the later stages of asphyxia, when, by the violent and convulsive action of the expiratory muscles, pressure is indirectly made on the lungs, and the circulation through them is proportionally interfered with.

(2) Accumulation of blood, with consequent distension of the right side of the heart and systemic veins, is the direct result, at least in part, of the obstruction to the pulmonary circulation just referred to. Other causes, however, are in operation. (*a*) The

* This term is, unfortunately, often applied to conditions of *dyspnœa* or *asphyxia;* but the modern application of the term, as in the text, is the more convenient.

vaso-motor centre (p. 189) stimulated by blood deficient in oxygen, causes contraction of all the small arteries with increase of arterial tension, and as an immediate consequence the filling of the systemic veins. (*b*) The increased arterial tension is followed by inhibition of the action of the heart, and, thus, the latter, contracting less frequently, and gradually enfeebled also by deficient supply of oxygen, becomes over-distended by blood which it cannot expel. At this stage the left as well as the right cavities are distended with blood.*

The ill effects of these conditions are to be looked for partly in the heart, the muscular fibres of which, like those of the urinary bladder or any other hollow muscular organ, are paralysed by over-stretching; and partly in the venous congestion, and consequent interference with the function of the higher nerve centres, especially the medulla oblongata.

(3) The passage of non-aërated blood through the lungs and its distribution over the body are events incompatible with life, in one of the higher animals, for more than a few minutes; the rapidity with which death ensues in asphyxia being due, more particularly, to the effect of non-oxygenised blood on the medulla oblongata, and, through the coronary arteries, on the muscular substance of the heart. The excitability of both nervous and muscular tissue is dependent on a constant and large supply of oxygen, and, when this is interfered with, is rapidly lost.

In some experiments performed by a committee appointed by the Medico-Chirurgical Society to investigate the subject of Suspended Animation, it was found that, in the dog, during simple asphyxia, *i.e.*, by simple privation of air, as by plugging the trachea, the average duration of the respiratory movements after the animal had been deprived of air, was 4 minutes 5 seconds; the extremes being 3 minutes 30 seconds, and 4 minutes 40 seconds. The average duration of the heart's action, on the other hand, was 7 minutes 11 seconds; the extremes being 6 minutes 40 seconds, and 7 minutes 45 seconds. It would seem, therefore, that on an average, the heart's action continues for 3 minutes 15 seconds after the animal has ceased to make respiratory efforts. A very similar relation was observed in the rabbit. Recovery never took place after the heart's action had ceased.

* See "Handbook for the Physiological Laboratory," by Dr. Burdon-Sanderson, p. 322.

The results obtained by the committee on the subject of drowning were very remarkable, especially in this respect, that whereas an animal may recover, after simple deprivation of air for nearly four minutes, yet, after submersion in water for 1½ minute, recovery seems to be impossible. This remarkable difference was found to be due, not to the mere submersion, nor directly to the struggles of the animal, nor to depression of temperature, but to the two facts, that in drowning, a free passage is allowed to air out of the lungs, and a free entrance of water into them. In proof of the correctness of this explanation it was found that when two dogs of the same size, one, however, having his windpipe plugged, the other not, were submerged at the same moment, and taken out after being under water for 2 minutes, the former recovered on removal of the plug, the latter did not. It is probably to the entrance of water into the lungs that the speedy death in drowning is mainly due. The results of *post-mortem* examination strongly support this view. On examining the lungs of animals deprived of air by plugging the trachea, they were found simply congested; but in the animals drowned, not only was the congestion much more intense, accompanied with ecchymosed points on the surface and in the substance of the lung, but the air tubes were completely choked up with a sanious foam, consisting of blood, water, and mucus, churned up with the air in the lungs by the respiratory efforts of the animal. The lung-substance, too, appeared to be saturated and sodden with water, which, stained slightly with blood, poured out at any point where a section was made. The lung thus sodden with water was heavy (though it floated), doughy, pitted on pressure, and was incapable of collapsing. It is not difficult to understand how, by such infarction of the tubes, air is debarred from reaching the pulmonary cells: indeed the inability of the lungs to collapse on opening the chest is a proof of the obstruction which the froth occupying the air-tubes offers to the transit of air. The entire dependence of the early fatal issue, in asphyxia by drowning, upon the open condition of the windpipe, and its results, was also strikingly shown by the following experiment. A strong dog had its windpipe plugged, and was then submerged in water for four minutes; in three quarters of a minute after its release it began to breathe, and in four minutes had fully recovered. This experiment was repeated with similar results on other dogs. When the entrance of water into the lungs, and its drawing up with the air into the bronchial tubes by means of the respiratory efforts, were diminished, as by rendering the animal insensible by chloroform previously to immersion, and thus depriving it of the power of making violent respiratory efforts, it was found that it could bear immersion for a longer period without dying than when not thus rendered insensible. Probably to a like diminution in the respiratory efforts, may also be ascribed the greater length of time persons have been found to bear submersion without being killed, when in a state of intoxication, poisoning by narcotics, or during insensibility from syncope.

We must carefully distinguish the asphyxiating effect of carbonic acid from the directly poisonous action of such gases as carbonic oxide or common coal-gas. The fatal effects often produced by carbonic oxide (as in accidents from burning char-

coal stoves in small, close rooms), are due to its entering into combination with the hæmoglobin of the blood-corpuscles (p. 118), and thus expelling the oxygen.

CHAPTER IX.

ANIMAL HEAT.

THE average temperature of the human body in those internal parts which are most easily accessible, as the mouth and rectum, is from 98·5° to 99·5° F.

In different parts of the *external* surface of the human body the temperature varies only to the extent of two or three degrees, when all are alike protected from cooling influences; and the difference which under these circumstances exists, depends chiefly upon the different degrees of blood-supply. In the arm-pit—the most convenient situation, under ordinary circumstances, for examination by the thermometer—the average temperature is 98·6° F.

The temperature varies in different internal parts, by one or two degrees; those parts and organs being warmest which contain most blood, and in which there occurs the greatest amount of chemical change. Thus the glands and the muscles are the warmest for this reason, and their temperature is highest, of course, when they are most actively working: while those tissues which, subserving only a mechanical function, are the seat of least active circulation and chemical change, are the coolest. These differences of temperature, however, are actually but slight, on account of the provisions which exist for maintaining uniformity of temperature in different parts (p. 268).

The chief circumstances by which the temperature of the healthy body is influenced are the following:—

Age; Sex; Period of the day; Exercise; Climate and Season; Food and Drink.

Age.—The average temperature of the new-born child is only about 1° F. above that proper to the adult; and the difference becomes still more trifling during infancy and early childhood. According to Wunderlich, the tempe-

rature falls to the extent of about $\frac{1}{5}$° to $\frac{1}{2}$° F. from early infancy to puberty, and by about the same amount from puberty to fifty or sixty years of age. In old age the temperature again rises, and approaches that of infancy.

Although the average temperature of the body, however, is not lower than that of younger persons, yet the power of resisting cold is less in them—exposure to a low temperature causing a greater reduction of heat than in young persons.

The same rapid diminution of temperature was observed by M. Edwards in the new-born young of most carnivorous and rodent animals when they were removed from the parent, the temperature of the atmosphere being between 50° and 53½° F.; whereas, while lying close to the body of the mother, their temperature was only 2 or 3 degrees lower than hers. The same law applies to the young of birds. Young sparrows, a week after they were hatched, had a temperature of 95° to 97°, while in the nest; but when taken from it, their temperature fell in one hour to 66½°, the temperature of the atmosphere being at the time 62½°. It appears from his investigations, that in respect of the power of generating heat, some mammalia are born in a less developed condition than others; and that the young of dogs, cats, and rabbits, for example, are inferior to the young of those animals which are not born blind. The need of external warmth to keep up the temperature of new-born children is well known; the researches of M. Edwards show, that the want of it is, as Hunter suggested, a much more frequent cause of death in new-born children than is generally supposed, and furnish a strong argument against the idea, that children, by early exposure to cold, can soon be hardened into resisting its injurious influence.

Sex.—The average temperature of the female would appear from observations by Dr. Ogle to be very slightly higher than that of the male.

Period of the Day.—The temperature undergoes a gradual alteration, to the extent of about 1° to 1½° F. in the course of the day and night; the *minimum* being at night or in the early morning, the *maximum* late in the afternoon.

Exercise.—*Active exercise* raises the temperature of the body from 1° to 2° F. (J. Davy, Clifford Allbutt). This may be partly ascribed to generally increased combustion-processes, and partly to the fact, that every muscular contraction is attended by the development of one or two degrees of heat in the acting muscle; and that the heat is increased according to the number and rapidity of these contractions, and is quickly diffused by the blood circulating from the heated muscles. Possibly, also, some heat may be generated in the various movements, stretchings, and recoilings of the other tissues, as the arteries, whose elastic walls, alternately dilated and contracted, may give out some heat, just as caoutchouc alternately stretched and recoiling becomes hot. But the heat thus developed cannot be great.

The great apparent increase of heat during exercise depends, in a great measure, on the increased circulation and quantity of blood, and, therefore, greater heat, in parts of the body (as the skin, and especially the skin of the extremities), which, at the same time that they feel more acutely than others any changes of temperature, are, under ordinary conditions, by some degrees colder than organs more centrally situated.

Climate and Season.—In passing from a temperate to a hot climate the temperature of the human body rises slightly, the increase rarely exceeding

2° to 3° F. In summer the temperature of the body is a little higher than in winter; the difference amounting to from $\frac{1}{8}$ to $\frac{1}{3}$° F. (Wunderlich.)

The same effects are observable in alterations of temperature not depending on season or climate.

Food and Drink.—The effect of a meal upon the temperature of a body is but small. A very slight rise usually occurs.

Cold alcoholic drinks depress the temperature somewhat ($\frac{1}{2}$° to 1° F.). Warm alcoholic drinks, as well as warm tea and coffee, raise the temperature (about $\frac{1}{2}$° F.).

In disease the temperature of the body deviates from the normal standard to a greater extent than would be anticipated from the slight effect of external conditions during health. Thus, in some diseases, as pneumonia and typhus, it occasionally rises as high as 106° or 107° F.; and considerably higher temperatures have been noted. In a case of malignant fever recorded by Dr. Norman Moore, the temperature in the axilla rapidly rose to 111° F., when the patient died. A temperature of 112·5° F. was observed by Wunderlich, in a case of idiopathic tetanus, at the time of death. In Asiatic cholera a thermometer placed in the mouth sometimes rises only to 77° or 79°; and in a case of tubercular meningitis, observed by Dr. Gee, the temperature of the rectum remained for hours at 79·4° F.

The temperature maintained by Mammalia in an active state of life, according to the tables of Tiedemann and Rudolphi, averages 101°. The extremes recorded by them were 96° and 106°, the former in the narwhal, the latter in a bat (Vespertilio Pipistrella). In Birds, the average is as high as 107°; the highest temperature, 111·25°, being in the small species, the linnets, &c. Among Reptiles, Dr. John Davy found, that while the medium they were in was 75°, their average temperature was 82·5°. As a general rule, their temperature, though it falls with that of the surrounding medium, is, in temperate media, two or more degrees higher; and though it rises also with that of the medium, yet at very high degrees it ceases to do so, and remains even lower than that of the medium. Fish and Invertebrata present, as a general rule, the same temperature as the medium in which they live, whether that be high or low; only among fish, the tunny tribe, with strong hearts and red meat-like muscles, and more blood than the average of fish have, are generally 7° warmer than the water around them.

The difference, therefore, between what are commonly called the warm- and the cold-blooded animals, is not one of absolutely higher or lower temperature; for the animals which to us, in a temperate climate, feel cold (being like the air or water, colder than the surface of our bodies), would, in an external temperature of 100°, have nearly the same temperature and feel hot to us. The real difference is, as Mr. Hunter expressed it, that what we call warm-blooded animals (Birds and Mammalia), have a certain "permanent heat in all atmospheres," while the temperature of the others, which we call cold-blooded, is "variable with every atmosphere."

The power of maintaining a uniform temperature, which Mammalia and Birds possess, is combined with the want of power to endure such changes of temperature of their bodies as are harmless to the other classes; and when their power of resisting change of temperature ceases, they suffer serious disturbances or die.

Sources and Mode of Production of Heat in the Body.

In explaining the chemical changes effected in the process of respiration (p. 251), it was stated that the oxygen of the atmosphere taken into the blood is combined, in the course of the circulation, with the carbon and the hydrogen of disintegrated and absorbed tissues, and of certain elements of food which have not been converted into tissues. That such a combination between the oxygen of the atmosphere and the carbon and hydrogen in the blood, is continually taking place, is made certain by the fact, that a larger amount of carbon and hydrogen is constantly being added to the blood from the food than is required for the ordinary purposes of nutrition, and that a quantity of oxygen is also constantly being absorbed from the air in the lungs, of the disposal of which no account can be given except by regarding it as combining, for the most part, with the excess of carbon and hydrogen, and being excreted in the form of carbonic acid and water. In other words, the blood of warm-blooded animals appears to be always receiving from the digestive canal and the lungs more carbon, hydrogen, and oxygen than are consumed in the repair of the tissues, and to be always emitting carbonic acid and water, for which there is no other known source than the combination of these elements.* By such combination, heat is continually produced in the animal body.

It is not, indeed, necessary to assume that the combustion processes, which ultimately issue in the production of carbonic acid and water, are as simple as the bare statement of the fact might seem to indicate. But complicated as the various stages of combustion of organic matter in the blood and tissues may be, the ultimate result is as simple as in ordinary combustion outside the body, and the products are the same. The same amount of heat will be evolved in the union of any given quantities of carbon and oxygen, and of hydrogen and oxygen, whether the combination be rapid and evident, as in ordinary combustion, or slow and imperceptible, as in the changes which occur in the

* Some heat will also be generated in the combination of sulphur and phosphorus with oxygen, to which reference has been made (p. 247); but the amount thus produced is but small.

living body. And since the heat thus arising will be generated wherever the blood is carried, every part of the body will be heated equally, or nearly so.

This theory, that the maintenance of the temperature of the living body depends on continual chemical change, chiefly by oxidation, of combustible materials existing in the tissues and in the blood, has long been established by the demonstration that the quantity of carbon and hydrogen which, in a given time, unites in the body with oxygen, is sufficient to account for the amount of heat generated in the animal within the same time: an amount capable of maintaining the temperature of the body at from 98° to 100°, notwithstanding a large loss by radiation and evaporation.

Many things observed in the economy and habits of animals are explicable by this theory, and may here briefly be quoted, although no longer required as additional evidence for its truth. Thus, as a general rule, in the various classes of animals, as well as in individual examples of each class, the quantity of heat generated in the body is in direct proportion to the activity of the respiratory process. The highest animal temperature, for example, is found in birds, in whom the function of respiration is most actively performed. In mammalia, the process of respiration is less active, and the average temperature of the body less, than in birds. In reptiles, both the respiration and the heat are at a much lower standard; while in animals below them, in which the function of respiration is at the lowest point, a power of producing heat is, in ordinary circumstances, hardly discernible. Among these lower animals, however, the observations of Mr. Newport supply confirmatory evidence. He shows that the larva, in which the respiratory organs are smaller in comparison with the size of the body, has a lower temperature than the perfect insect. Volant insects have the highest temperature, and they have always the largest respiratory organs and breathe the greatest quantity of air; while among terrestrial insects, those also produce the most heat which have the largest respiratory organs and breathe the most air. During sleep, hybernation, and other states of inaction, respiration is slower or suspended, and the temperature is proportionately diminished; while, on the other hand, when the insect is most active and respiring most voluminously, its amount of temperature is at its maximum, and corresponds with the quantity of respiration. Neither the rapidity of the circulation, nor the size of the nervous system, according to Mr. Newport, presents such a constant relation to the evolution of heat.

On the Regulation of the Temperature of the Human Body.

The continual production of heat in the body has been already referred to. There is also, of necessity, a continual loss. But

in healthy warm-blooded animals the loss and gain of heat are so nearly balanced one by the other, that under all ordinary circumstances, an uniform temperature, within two or three degrees, is preserved.

The loss of heat from the human body takes place chiefly by radiation and conduction from its surface, and by means of the constant evaporation of water from the same part, and from the air-passages. In each act of respiration, heat is also lost by so much warmth as the expired air acquires (p. 244). All food and drink which enter the body at a lower temperature than itself abstract also a small measure of heat: while the urine and fæces which leave the body at about its own temperature are also means by which a small amount is lost.

By far the most important loss of heat from the body,—probably 80 or 90 per cent. of the whole amount, is that which takes place by radiation, conduction, and evaporation from the skin. And it is to this part especially, and in a smaller measure to the air-passages, that we must look for the means by which the temperature is regulated; in other words, by which it is prevented from rising beyond the normal point on the one hand, or sinking below it on the other. The chief indirect means for accomplishing the same end are, variations in the amount and quality of the food and drink taken, variations in clothing, and in exposure to external heat or cold.

In order to understand the means by which the heat of the body is regulated, it is necessary to take into consideration the following facts: First, the immediate source of heat in the body is the presence of a large quantity of a warm fluid—the blood, the temperature of which is, in health, about 100° F. In the second place, the blood, while constantly moving in a multitude of different streams, is every minute or so, gathered up in the heart, into one large stream, before being again dispersed to all parts of the body. In this way, the temperature of the blood remains almost exactly the same in all parts; for while a portion of it in passing through one organ, as the skin, may become cooler, and through another organ, as the liver, may become warmer, the effect on each separate stream is more

or less neutralized when it mingles with another, and an average is struck, so to speak, for all the streams when they form one, in passing through the heart. Uniformity of temperature is maintained also by the contiguity and continuity of the various organs and tissues one with another.

The means by which the skin is able to act as one of the most important organs for regulating the temperature of the blood, are—(1), that it offers a large surface for radiation, conduction, and evaporation; (2), that it contains a large amount of blood; (3), that the quantity of blood contained in it is the greater under those circumstances which demand a loss of heat from the body, and *vice versâ*. For the circumstance which directly determines the quantity of blood in the skin, is that which governs the supply of blood to all the tissues and organs of the body, namely, the power of the vaso-motor nerves to cause a greater or less tension of the muscular element in the walls of the arteries (see p. 188), and, in correspondence with this, a lessening or increase of the calibre of the vessel, accompanied by a less or greater current of blood. A warm or hot atmosphere so acts on the nerve fibres of the skin, as to lead them to cause in turn a relaxation of the muscular fibre of the blood-vessels; and, as a result, the skin becomes full-blooded, hot, and sweating; and much heat is lost. With a low temperature, on the other hand, the blood-vessels shrink, and in accordance with the consequently diminished blood-supply, the skin becomes pale, and cold, and dry. Thus, by means of a self-regulating apparatus, the skin becomes the most important of the means by which the temperature of the body is regulated.

In connection with loss of heat by the skin, reference has been made to that which occurs both by radiation and conduction, and by evaporation; and the subject of animal heat has been considered almost solely with regard to the ordinary case of man living in a medium colder than his body, and therefore losing heat in all the ways mentioned. The importance of the means, however, adopted, so to speak, by the skin for regulating the temperature of the body, will depend on the conditions by which it is surrounded; an inverse proportion existing in most cases

between the loss by radiation and conduction on the one hand, and by evaporation on the other. Indeed, the small loss of heat by evaporation in cold climates may go far to compensate for the greater loss by radiation; as, on the other hand, the great amount of fluid evaporated in hot air may remove nearly as much heat as is commonly lost by both radiation and evaporation in ordinary temperatures; and thus, it is possible, that the quantities of heat required for the maintenance of an uniform proper temperature in various climates and seasons are not so different as they, at first thought, seem.

Many examples might be given of the power which the body possesses of resisting the effects of a high temperature, in virtue of evaporation from the skin.

Sir Charles Blagden and others supported a temperature varying between 198° and 211° F. in dry air for several minutes; and in a subsequent experiment he remained eight minutes in a temperature of 260°.

"The workmen of Sir F. Chantrey were accustomed to enter a furnace, in which his moulds were dried, whilst the floor was red-hot, and a thermometer in the air stood at 350°; and Chabert, the fire-king, was in the habit of entering an oven the temperature of which was from 400° to 600°." (Carpenter).

But such heats are not tolerable when the air is moist as well as hot, so as to prevent evaporation from the body. Mr. C. James states, that in the vapour baths of Nero he was almost suffocated in a temperature of 112°, while in the caves of Testaccio, in which the air is dry, he was but little incommoded by a temperature of 176°. In the former, evaporation from the skin was impossible; in the latter it was abundant, and the layer of vapour which would rise from all the surface of the body would, by its very slowly conducting power, defend it for a time from the full action of the external heat.

(The glandular apparatus, by which secretion of fluid from the skin is effected, will be considered in the Section on the Skin.)

The ways by which the skin may be rendered more efficient as a cooling-apparatus by exposure, by baths, and by other means which man instinctively adopts for lowering his temperature when necessary, are too well known to need more than to be mentioned.

Although, under ordinary circumstances, the external application of cold only temporarily depresses the temperature to a slight extent, it is otherwise in cases of high temperature (107—108°) in fever. In these cases a tepid

bath (80°) may reduce the temperature several degrees, and the effect so produced lasts for many hours.

As a means for lowering the temperature, the lungs and air-passages are very inferior to the skin; although, by giving heat to the air we breathe, they stand next to the skin in importance. As a *regulating* power, the inferiority is still more marked. The air which is expelled from the lungs leaves the body at about the temperature of the blood, and is always saturated with moisture. No inverse proportion, therefore, exists between the loss of heat by radiation and conduction on the one hand, and by evaporation on the other. The colder the air, for example, the greater will be the loss in all ways. Neither is the quantity of blood which is exposed to the cooling influence of the air diminished or increased, so far as is known, in accordance with any need in relation to temperature. It is true that by varying the number and depth of the respirations, the quantity of heat given off by the lungs may be made, to some extent, to vary also. But the respiratory passages, while they must be considered important means by which heat is lost, are altogether subordinate in the power of regulating the temperature, to the skin.

It may seem to have been assumed, in the foregoing pages, that the only regulating apparatus for temperature required by the human body is one that shall, more or less, produce a *cooling* effect; and as if the amount of heat produced were always, therefore, in excess of that which is required. Such an assumption would be incorrect. We have the power of regulating the production of heat, as well as its loss.

In *food* we have a means for elevating our temperature. It is the fuel, indeed, on which animal heat ultimately depends altogether. Thus, when more heat is wanted, we instinctively take more food, and take such kinds of it as are good for combustion; while every-day experience shows the different power of resisting cold possessed respectively, by the well-fed and by the starved.

In northern regions, again, and in the colder seasons of more southern climes, the quantity of food consumed is (speaking very generally) greater than that consumed by the same men or animals in opposite conditions of climate and season. And the food

which appears naturally adapted to the inhabitants of the coldest climates, such as the several fatty and oily substances, abounds in carbon and hydrogen, and is fitted to combine with the large quantities of oxygen which, breathing cold dense air, they absorb from their lungs.

In exercise, again, we have an important means of raising the temperature of our bodies (p. 264).

The influence of *external coverings* for the body must not be unnoticed. In warm-blooded animals, they are always adapted, among other purposes, to the maintenance of uniform temperature; and man adapts for himself such as are, for the same purpose, fitted to the various climates to which he is exposed. By their means, and by his command over food and fire, he maintains his temperature on all accessible parts of the surface of the earth.

The *influence of the nervous system* in modifying the production of heat has been already referred to. The experiments and observations which best illustrate it are those showing, first, that when the supply of nervous influence to a part is cut off, the temperature of that part falls below its ordinary degree; and, secondly, that when death is caused by severe injury to, or removal of, the nervous centres, the temperature of the body rapidly falls, even though artificial respiration be performed, the circulation maintained, and to all appearance the ordinary chemical changes of the body be completely effected. It has been repeatedly noticed, that after division of the nerves of a limb its temperature falls; and this diminution of heat has been remarked still more plainly in limbs deprived of nervous influence by paralysis. For example, Mr. Earle found the temperature of the hand of a paralysed arm to be 70°, while the hand of the sound side had a temperature of 92° F. On electrifying the paralysed limb, the temperature rose to 77°. In another case, the temperature of the paralysed finger was 56° F., while that of the unaffected hand was 62°.

With equal certainty, though less definitely, the influence of the nervous system on the production of heat, is shown in the rapid and momentary increase of temperature, sometimes general,

at other times quite local, which is observed in states of nervous excitement; in the general increase of warmth of the body, sometimes amounting to perspiration, which is excited by passions of the mind; in the sudden rush of heat to the face, which is not a mere sensation; and in the equally rapid diminution of temperature in the depressing passions. But none of these instances suffice to prove that heat is generated by mere nervous action, independent of any chemical change; all are explicable, on the supposition that the nervous system alters, by its power of controlling the calibre of the blood-vessels (p. 188), the quantity of blood supplied to a part; while any influence which the nervous system may have in the production of heat, apart from this influence on the blood-vessels, is an indirect one, and is derived from its power of causing nutritive change in the tissues, which may, by involving the necessity of chemical action, involve the production of heat. The existence of nerves which regulate animal heat otherwise than by their influence in trophic (nutritive) or vaso-motor changes, although by many considered probable, is not yet proven.

In connection with the regulation of animal temperature, and its maintenance in health at the normal height, may be noted the result of circumstances too powerful, either in raising or lowering the heat of the body, to be controlled by the proper regulating apparatus. Walther found that rabbits and dogs, when tied to a board and exposed to a hot sun, reached a temperature of 114·8° F., and then died. Cases of sunstroke furnish us with similar examples in the case of man; for it would seem that here death ensues chiefly or solely from elevation of the temperature. In a case related by Dr. Gee, the temperature in the axilla was 109·5° F.; and in many febrile diseases the immediate cause of death appears to be the elevation of the temperature to a point inconsistent with the continuance of life.

The effect of mere loss of bodily temperature in man is less well known than the effect of heat.

From experiments by Walther, it appears that rabbits can be cooled down to 48° F. before they die, if artificial respiration be

kept up. Cooled down to 64° F., they cannot recover unless external warmth be applied together with the employment of artificial respiration. Rabbits not cooled below 77° F. recover by external warmth alone.

CHAPTER X.

DIGESTION.

Digestion is the process by which the materials of our food are so changed as to be made fit for absorption and addition to the blood.

Food.

The following is a convenient tabular classification of the usual and necessary kinds of food:—

Organic.	NITROGENOUS:— Proteids, as Albumen, Casein, Syntonin, Gluten, and their allies, and Gelatin (containing Carbon, Hydrogen, Oxygen, and Nitrogen; some of them, also Sulphur and Phosphorus). NON-NITROGENOUS:— (1). Amyloids—Starch, Sugar, and their allies (containing Carbon, Hydrogen, and Oxygen). (2). Oils and Fats (containing Carbon, Hydrogen, and Oxygen; the Oxygen in much smaller proportion than in starch or sugar).
Inorganic.	(3). Mineral or Saline Matters; as Chloride of Sodium, Phosphate of Calcium, &c. (4). Water.

Animals require, for food, both *organic* and *inorganic* substances; the apparent sustenance of life and health on a diet composed of the first-named group only being due to the fact that inorganic substances are contained in all the natural organic foods. Pure fibrin, pure gelatin, and other organic principles purified from the inorganic substances naturally mingled with them, are incapable of supporting life for more than a brief time.

Moreover, health cannot be maintained by any number of substances derived exclusively from one only of the two groups of

organic alimentary principles mentioned above. A mixture of nitrogenous and non-nitrogenous organic substances, together with the inorganic principles which are severally contained in them, is essential to the well-being, and, generally, even to the existence of an animal. The truth of this has been demonstrated by experiments, and is illustrated also by the composition of those foods which are sufficient by themselves for the maintenance of life. Milk and eggs are good examples of this.

COMPOSITION OF MILK.

	Human.	Cows'.
Water	890	858
Solids	110	142
	1,000	1,000
Casein	35	68
Butter	25	38
Sugar (with extractives)	48	30
Salts	2	6
	110	142

In milk, as will be seen from the preceding table, the albuminous group of aliments is represented by the casein, the oleaginous by the butter, the aqueous by the water, the saccharine by the sugar of milk. Among the salts of milk are likewise phosphate of calcium, alkaline and other salts, and a trace of iron; so that it may be briefly said to include all the substances which the tissues of the growing animal need for their nutrition, and which are required for the production of animal heat.

The yelk and albumen of eggs are in the same relation as food for the embryoes of oviparous animals, that milk is to the young of Mammalia, and afford another example of the necessity for a mixture of various alimentary principles.

COMPOSITION OF FOWLS' EGGS.

	White.	Yelk.
Water	78	52
Nitrogenous matter	20·4	16
Fatty matter	—	30·7
Salts	1·6	1·3
	100·0	100·0

Experiments illustrating the same principle have been performed by Magendie and others.

Dogs were fed exclusively on sugar and distilled water. During the first seven or eight days they were brisk and active, and took their food and drink as usual; but in the course of the second week, they began to get thin, although their appetite continued good, and they took daily between six and eight ounces of sugar. The emaciation increased during the third week, and they became feeble, and lost their activity and appetite. At the same time an ulcer formed on each cornea, followed by an escape of the humours of the eye: this took place in repeated experiments. The animals still continued to eat three or four ounces of sugar daily; but became at length so feeble as to be incapable of motion, and died on a day varying from the thirty-first to the thirty-fourth. On dissection, their bodies presented all the appearances produced by death from starvation; indeed, dogs will live almost the same length of time without any food at all.

When dogs were fed exclusively on gum, results almost similar to the above ensued. When they were kept on olive-oil and water, all the phenomena produced were the same, except that no ulceration of the cornea took place: the effects were also the same with butter. The experiments of Chossat and Letellier prove the same; and in men, the same is shown by the various diseases to which they who consume but little nitrogenous food are liable, and especially, as Dr. Budd has shown, by the affection of the cornea which is observed in Hindus feeding almost exclusively on rice. But it is not only the non-nitrogenous substances, which, taken alone, are insufficient for the maintenance of health. The experiments of the Academies of France and Amsterdam were equally conclusive that gelatin alone soon ceases to be nutritive.

Mr. Savory's observations on food confirm and extend the results obtained by Magendie, Chossat, and others. They show that animals fed exclusively on non-nitrogenous diet speedily emaciate and die, as if from starvation; that life is much more prolonged in those fed with nitrogenous than by those with non-nitrogenous food; and that animal heat is maintained as well by the former as by the latter—a fact which proves that nitrogenous elements of food, as well as non-nitrogenous, may be regarded as calorifacient.

Man is supported as well by food constituted wholly of animal substances, as by that which is formed entirely of vegetable matters, on the condition, of course, that it contain a mixture of the various nitrogenous and non-nitrogenous substances just shown to be essential for healthy nutrition.

In the case of carnivorous animals, the food upon which they exist, consisting as it does of the flesh and blood of other animals, not only contains all the elements of which their own blood and tissues are composed, but contains them combined, probably, in the same forms. Therefore, little more may seem requisite, in the preparation of this kind of food for the nutrition of the body, than that it should be dissolved and conveyed into the blood in a condition capable of being re-organised. But in the case of

the herbivorous animals, which feed exclusively upon vegetable substances, it might seem as if there would be greater difficulty in procuring food capable of assimilation into their blood and tissues. But the chief ordinary articles of vegetable food contain substances identical in composition with the albumen, fibrin, and casein, which constitute the principal nutritive materials in animal food. Albumen is abundant in the juices and seeds of nearly all vegetables; the gluten which exists, especially in corn and other seeds of grasses as well as in their juices, is identical in composition with fibrin, and is often named vegetable fibrin; and the substance named legumen, which is obtained especially from peas, beans, and other seeds of leguminous plants, and from the potato, is identical with the casein of milk. All these vegetable substances are, equally with the corresponding animal principles, and in the same manner, capable of conversion into blood and tissue; and as the blood and tissues in both classes of animals are alike, so also the nitrogenous food of both may be regarded as, in essential respects, similar.

It is in the relative quantities of the nitrogenous and non-nitrogenous compounds in these different foods that the difference lies, rather than in the presence of substances in one of them which do not exist in the other.

The only non-nitrogenous compounds in ordinary animal food are the fat, the saline matters, and water, and, in some instances, the vegetable matters which may chance to be in the digestive canals of such animals as are eaten whole. The amount of these, however, is altogether much less than that of the non-nitrogenous substances represented by the starch, sugar, gum, oil, etc., in the vegetable food of herbivorous animals.

Starvation.

The effects of total deprivation of food have been made the subject of experiments on the lower animals, and have been but too frequently illustrated in man.

(1). One of the most notable effects of starvation, as might be expected, is loss of weight; the loss being greatest at first, as a rule, but afterwards not varying very much, day by day, until death ensues. Chossat found that the ultimate proportional loss was, in different animals experimented on, almost exactly the same; death occurring when the body had lost two-fifths (forty per cent.) of its original weight.

Different parts of the body lose weight in very different proportions. The following results are taken, in round numbers, from the table given by M. Chossat:—

Fat loses	93	per cent.
Blood	75	"
Spleen	71	"
Pancreas	64	"

Liver loses	52 per cent.
Heart	44 „
Intestines	42 „
Muscles of locomotion	42 „
Stomach loses	39 „
Pharynx, Œsophagus	34 „
Skin	33 „
Kidneys	31 „
Respiratory apparatus	22 „
Bones	16 „
Eyes	10 „
Nervous system	2 „ (nearly

(2). The effect of starvation on the temperature of the various animals experimented on by Chossat was very marked. For some time the *variation* in the daily temperature was more marked than its absolute and continuous diminution, the daily fluctuation amounting to 5° or 6° F., instead of 1° or 2° F., as in health. But a short time before death, the temperature fell very rapidly, and death ensued when the loss had amounted to about 30° F. It has been often said, and with truth, although the statement requires some qualification, that death by starvation is really death by cold; for not only has it been found that differences of time with regard to the period of the fatal result are attended by the same ultimate loss of heat, but the effect of the application of external warmth to animals cold and dying from starvation, is more effectual in reviving them than the administration of food. In other words, an animal exhausted by deprivation of nourishment is unable so to digest food as to use it as fuel, and therefore is dependent for heat on its supply from without. Similar facts are often observed in the treatment of exhaustive diseases in man.

(3). The symptoms produced by starvation in the human subject are hunger, accompanied, or it may be replaced by pain, referred to the region of the stomach; insatiable thirst; sleeplessness; general weakness and emaciation. The exhalations both from the lungs and skin are fœtid, indicating the tendency to decomposition which belongs to badly-nourished tissues; and death occurs, sometimes after the additional exhaustion caused by diarrhœa, often with symptoms of nervous disorder, delirium, or convulsions.

(4). In the human subject death commonly occurs within six to ten days after total deprivation of food. But this period may be considerably prolonged by taking a very small quantity of food, or even water only. The cases so frequently related of survival after many days, or even some weeks, of abstinence, have been due either to the last-mentioned circumstances, or to others less effectual, which prevented the loss of heat and moisture. Cases in which life has continued after total abstinence from food and drink for many weeks, or months, exist only in the imagination of the vulgar.

(5). The appearances presented after death from starvation are those of general wasting and bloodlessness, the latter condition being least noticeable in the brain. The stomach and intestines are empty and contracted, and the walls of the latter appear remarkably thinned and almost transparent. The various secretions are scanty or absent, with the exception of the bile, which, somewhat concentrated, usually fills the gall-bladder. All parts of the body readily decompose.

It has just been remarked that man can live upon animal matters alone, or upon vegetables. The structure of his teeth, however, as well as experience, seems to declare that he is best fitted for a mixed diet; and the same inference may be readily gathered from other facts and considerations.

The food a man takes into his body daily, represents or ought to represent, the quantity and kind of matter necessary for replacing that which is daily cast out by the way of lungs, skin, kidneys, and other organs. To find out, therefore, the quantity and kind of food necessary for a healthy man, it will, evidently, be the best plan to consider in the first place what he loses by excretion.

For the sake of example, we may now take only two elements, carbon and nitrogen, and, if we discover what amount of these is respectively discharged in a given time from the body, we shall be in a position to judge what kind of food will most readily and economically replace their loss.

The quantity of carbon daily lost from the body amounts to about 4,500 grains, and of nitrogen 300 grains; and if a man could be fed by these elements, as such, the problem would be a very simple one; a corresponding weight of charcoal, and, allowing for the oxygen in it, of atmospheric air, would be all that is necessary. But, as before remarked, an animal can live only upon these elements when they are arranged in a particular manner with others, in the form of an organic compound, as albumen, starch, and

the like; and the relative proportion of carbon to nitrogen in either of these compounds alone, is, by no means, the proportion required in the diet of man. Thus, in albumen, the proportion of carbon to nitrogen is only as 3·5 to 1. If, therefore, a man took into his body, as food, sufficient albumen to supply him with the needful amount of carbon, he would receive more than four times as much nitrogen as he wanted; and if he took only sufficient to supply him with nitrogen, he would be starved for want of carbon. It is plain, therefore, that he should take with the albuminous part of his food, which contains so large a relative amount of nitrogen in proportion to the carbon he needs, substances in which the nitrogen exists in much smaller quantities.

Food of the latter kind is provided in such compounds as starch and fat. The latter indeed as it exists for the most part in considerable amount mingled with the flesh of animals, removes to a great extent, in a diet of animal food, the difficulty which would otherwise arise from a deficiency of carbon—fat containing a large relative proportion of this element, and no nitrogen.

To take another example; the proportion of carbon to nitrogen in bread is about 30 to 1. If a man's diet were confined to bread, he would eat, therefore, in order to obtain the requisite quantity of nitrogen, twice as much carbon as is necessary; and it is evident, that, in this instance, a certain quantity of a substance with a large relative amount of nitrogen is the kind of food necessary for redressing the balance.

To place the preceding facts in a tabular form, and taking meat as an example instead of pure albumen:—meat contains about 10 per cent. of carbon, and rather more than 3 per cent. of nitrogen. Supposing a man to take meat for the supply of the needful carbon, he would require 45,000 grains, or nearly 6½ lbs. containing:—

Carbon	4,500 grains
Nitrogen	1,350 "
Excess of Nitrogen above the amount required .	1,050 "

Bread contains about 30 per cent. of carbon and 1 per cent. of nitrogen.

If bread alone, therefore, were taken as food, a man would require, in order to obtain the requisite nitrogen, 30,000 grains, containing—

Carbon	9,000 grains
Nitrogen	300 "
Excess of Carbon above the amount required .	4,500 "

But a combination of bread and meat would supply much more economically what was necessary. Thus—

	Carbon.	Nitrogen.
15,000 grains of bread (or rather more than 2lb.) contain	4,500 grs.	150 grs.
5,000 grains of meat (or about ¾lb.) contain	500 "	150 "
	5,000 "	300 "

So that ¾ lb. of meat, and less than 2 lbs. of bread would supply all the needful carbon and nitrogen with but little waste.

From these facts it will be plain that a mixed diet is the best and most economical food for man; and the result of experience entirely coincides with what might have been anticipated on theoretical grounds only.

It must not be forgotten that the value of certain foods may depend quite as much on their digestibility as on the relative quantities of the necessary elements which they contain.

In actual practice, moreover, the quantity and kind of food to be taken with most economy and advantage cannot be settled for each individual, only by considerations of the exact quantities of certain elements that are required. Much will of necessity depend on the habits and digestive powers of the individual, on the state of his excretory organs, and on many other circumstances. Food which to one person is appropriate enough, may be quite unfit for another; and the changes of diet so instinctively practised by all to whom they are possible, have much more reliable grounds of justification than any which could be framed on theoretical considerations only.

In many of the experiments on the digestibility of various articles of food, disgust at the sameness of the diet may have had as much to do with inability to consume and digest it, as the want of nutritious properties in the substances which were experimented on. And that disease may occur from the want of particular food, is well shown by the occurrence of scurvy when fresh vegetables are deficient, and its rapid cure when they are again eaten: and the disease which is here so remarkably evident in its symptoms, causes, and cure, is matched by numberless other ailments, the causes of which, however, although analogous, are less exactly known, and therefore less easily combated.

With regard to the quantity, too, as well as the kind of food necessary, there will be much diversity in different individuals. Dr. Dalton believed, from some experiments which he performed, that the quantity of food necessary for a healthy man, taking free exercise in the open air, is as follows:—

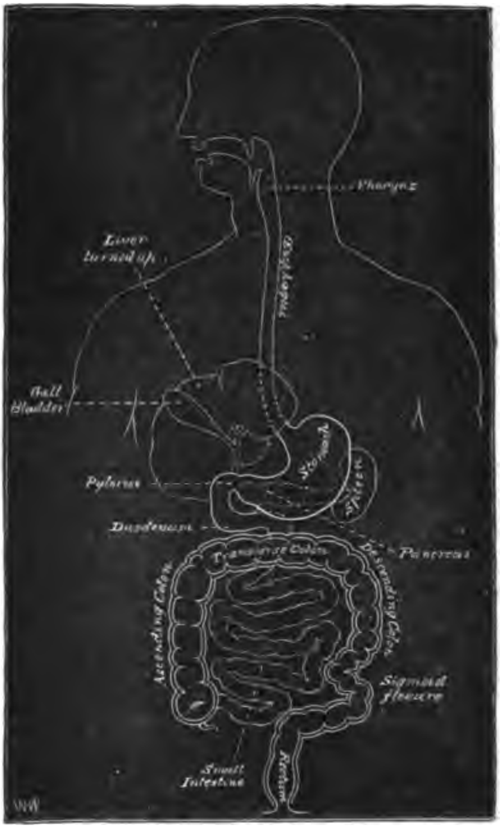
Meat	16 ounces,	or 1·00 lb. avoird.		
Bread	19 „	„ 1·19	„	„
Butter or Fat	$3\frac{1}{2}$ „	„ 0·22	„	„
Water	52 fluid ozs.	„ 3·38	„	„

The quantity of meat, however, here given is probably more in proportion to the other articles of diet enumerated than is needful for the majority of individuals under the circumstances stated.

PASSAGE OF FOOD THROUGH THE ALIMENTARY CANAL.

The course of the food through the alimentary canal of man will be readily seen from the accompanying diagram (fig. 134).

Fig. 134.*



* Fig. 134. Diagram of the Alimentary Canal. The *small* intestine of man is from about 3 to 4 times as long as the *large* intestine.

The food taken into the mouth passes thence through the œsophagus into the stomach, and from this into the small and large intestine successively; gradually losing, by absorption, the greater portion of its nutritive constituents. The residue, together with such matters as may have been added to it in its passage, is discharged from the rectum through the anus.

We shall now consider, in detail, the process of digestion, as it takes place in each stage of this journey of the food through the alimentary canal.

The Salivary Glands and the Saliva.

The first of a series of changes to which the food is subjected in the digestive canal, takes place in the cavity of the mouth. The solid articles of food are here submitted to the action of the teeth (p. 92), whereby they are divided and crushed, and by being at the same time mixed with the fluids of the mouth, are reduced to a soft pulp, capable of being easily swallowed. The fluids with which the food is mixed in the mouth consist of the secretion of the *salivary* glands, and the *mucous* glands which line the mouth.

Mastication and Insalivation.

The act of chewing or mastication is performed by the biting and grinding movement of the lower range of teeth against the upper. The simultaneous movements of the tongue and cheeks, assist partly by crushing the softer portions of the food against the hard palate, gums, &c., and thus supplementing the action of the teeth, and partly by returning the morsels of food to the action of the teeth, again and again, as they are squeezed out from between them, until they have been sufficiently chewed.

The simple up and down, or *biting* movements of the lower jaw, are performed by the *temporal*, *masseter*, and *internal pterygoid* muscles, the action of which in closing the jaws alternates with that of the digastric and other muscles passing from the os hyoides to the lower jaw, which open them. The *grinding* or side to side movements of the lower jaw are performed mainly by the *external pterygoid* muscles, the muscle of one side acting

alternately with the other. When both external pterygoids act together, the lower jaw is pulled directly forwards, so that the lower incisor teeth are brought in front of the level of the upper.

The act of mastication is much assisted by the saliva which is secreted in largely increased amount during the process, and the intimate incorporation of which with the food, as it is being chewed, is termed *insalivation*.

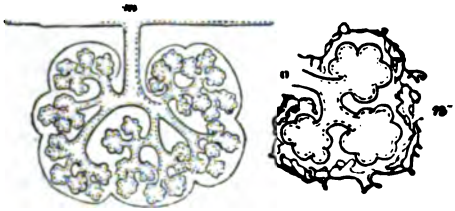
As in the case of so many other actions, that of mastication is partly voluntary, and partly reflex and involuntary. The consideration of such *sensori-motor* actions will come hereafter (see Chapter on the Nervous System). It will suffice here to state that the nerves chiefly concerned are the *sensory* branches of the fifth, and the glosso-pharyngeal, and the *motor* branches of the fifth and ninth (hypoglossal) cerebral nerves. The nerve-centre by which the reflex action occurs, and by which the movements of the various muscles are harmonised, is situate in the medulla oblongata. In so far as mastication is voluntary or mentally perceived, it becomes so under the influence, in addition to the medulla oblongata, of the cerebral hemispheres.

The function of the inter-articular fibro-cartilage of the temporo-maxillary joint in mastication may be here mentioned. (1) As an elastic pad it serves well to distribute the pressure caused by the exceedingly powerful action of the masticatory muscles. (2) It also serves as a joint-surface or socket for the condyle of the lower jaw, when the latter has been partially drawn forward out of the glenoid cavity of the temporal bone by the external pterygoid muscle, some of the fibres of the latter being attached to its front surface, and consequently drawing it forward with the condyle which moves on it.

The glands concerned in the production of *saliva*, are very extensive, and, in man and Mammalia generally, are presented in the form of four pairs of large glands, the parotid, submaxillary, sublingual, and numerous smaller bodies, of similar structure and with separate ducts, which are scattered thickly beneath the mucous membrane of the lips, cheeks, soft palate, and root of the tongue. The structure of all these glands is essentially the same. Each is composed of several parts, called

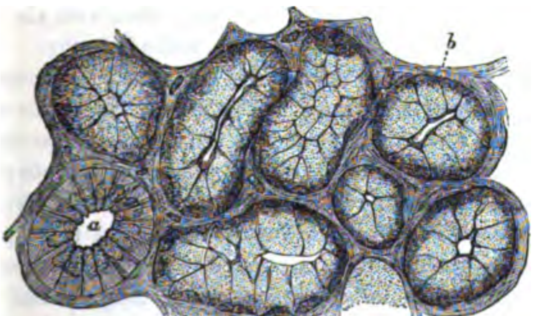
lobes, which are connected by areolar tissue; and each of these lobes, again, is made up of a number of smaller parts called

Fig. 135.*



lobules, bound together as before by areolar tissue. Each of these lobules is a miniature representation of the whole gland. It contains a small branch of the duct, which, subdividing, ends in small vesicular pouches, called *acini*, a group of which may be considered the dilated end of one of the smaller ducts (fig. 135, *n*).

Fig. 136.†



Each of the acini is about $\frac{1}{500}$ of an inch in diameter, and is formed of a fine structureless membrane, lined on the inner surface and often filled by spheroidal or glandular epithelium while on the outside is a plexus of capillary blood-vessels (fig. 136).

* Fig. 135. Diagram of a racemose or saccular compound gland; *m*, entire gland, showing branched duct and lobular structure; *n*, a lobule detached, with *o*, branch of duct proceeding from it (Sharpey).

† Fig. 136. Section of Submaxillary gland of dog. Showing gland-cells (*b*) and a duct, *a*, in section (Kölliker)

In the salivary glands of many animals besides man two distinct kinds of gland-cells—the "mucous" and "protoplasmic"—may be distinguished.

The mucous cells are closely packed in the acini while the protoplasmic cells, which are darker and strongly granulated, occupy the peripheral part of the acini like the peptic cells of the gastric glands (p. 300), which they resemble both in position and general appearance.

After prolonged irritation of the secreting nerves remarkable changes occur: the mucous cells discharge their contents in the saliva, and the gland is now found to be filled with protoplasmic cells; these multiply rapidly by division and many of them by a transformation of their cell-contents into mucin become mucous cells, thus restoring the gland to its original condition (Heidenhain).

According to Pflüger's researches some of the terminal filaments of the nerves which enter the submaxillary gland actually enter the substance of the secreting cells and end in their nuclei; but these observations require further confirmation before they can be finally accepted.

Independently of them there seem strong grounds for accepting the view that the *chorda tympani* contains "secreting fibres" which directly influence the gland cells, in addition to the vaso-inhibitory fibres whose stimulation causes an increased blood supply and consequently an increased secretion (p. 289).

Saliva, as it commonly flows from the mouth, is mixed with the secretion of the *mucous glands*, and often with air bubbles, which, being retained by its viscidity, make it frothy.

When obtained from the parotid ducts, and free from mucus, saliva is a transparent watery fluid, the specific gravity of which varies from 1·004 to 1·008, and in which, when examined with the microscope, are found floating a number of minute particles, derived from the secreting ducts and vesicles of the glands. In the impure or mixed saliva are found, besides these particles, numerous epithelial scales separated from the surface of the mucous membrane of the mouth and tongue, and mucus-corpuscles, discharged probably from the mucous glands of the mouth and the tonsils, which, when the saliva is collected in a deep vessel, and left at rest, subside in the form of a white opaque matter, leaving the supernatant salivary fluid transparent and colourless, or with a pale bluish-grey tint. In *reaction*, the saliva, when first secreted appears to be always alkaline; and that from the parotid gland is said to be more strongly alkaline than that from the other salivary glands. This alkaline condition is most evident when digestion is going on, and according to Dr. Wright, the degree of alkalinity of the saliva bears a

direct proportion to the acidity of the gastric fluid secreted at the same time. During fasting, the saliva, although secreted alkaline, shortly becomes neutral; and it does so especially when secreted slowly and allowed to mix with the acid mucous of the mouth, by which its alkaline reaction is neutralised.

The following analysis of the saliva is by Frerichs:—

Composition of Saliva.

Water		994·10
Solids		5·90
Ptyalin	1·41	
Fat	0·07	
Epithelium and Mucus	2·13	
Salts:—		
Sulpho-Cyanide of Potassium	2·29	
Sodium Phosphate		
Calcium Phosphate		
Magnesium Phosphate		
Sodium Chloride		
Potassium Chloride		
	5·90	

The rate at which saliva is secreted is subject to considerable variation. When the tongue and muscles concerned in mastication are at rest, and the nerves of the mouth are subject to no unusual stimulus, the quantity secreted is not more than sufficient, with the mucus, to keep the mouth moist. But the flow is much accelerated when the movements of mastication take place, and especially when they are combined with the presence of food in the mouth. It may be excited also, even when the mouth is at rest, by the mental impressions produced by the sight or thought of food; also by the introduction of food into the stomach. The influence of the latter circumstance was well shown in a case mentioned by Dr. Gairdner, of a man whose pharynx had been divided: the injection of a meal of broth into the stomach was followed by the secretion of from six to eight ounces of saliva.

Under these varying circumstances, the *quantity* of saliva secreted in twenty-four hours varies also; its average amount is probably from 1 to 2 lbs. (Harley).

The process of secretion in the salivary glands is identical with that of glands in general (see chapter on Secretion); the cells which line the ultimate branches of the ducts (*b*, fig. 136) being the agents by which the special constituents of the saliva are formed. The process may be compared with that of growth, inasmuch as these cells grow and develope as they take up into their substance the materials of the secretion they are destined to form. Their most highly developed condition, however, is but transitory. The materials which they have incorporated with themselves are almost at once given up again, in the form of a fluid (secretion), which escapes from the ducts of the gland; and the cells, themselves, to what extent it is not known, undergo disintegration,—again to be renewed, in the intervals of the active exercise of their functions. The source whence the cells obtain the materials of their secretion, is the blood, or, to speak more accurately, the plasma which is filtered off from the circulating blood into the interstices of all living textures.

The secretion of saliva is probably continuous, but it is very largely increased during the period of digestion; and the condition of the glands corresponds with the difference. During digestion the process of secretion is in excess; while in the intervals the growth of the cells is in excess of their disintegration. These facts have been confirmed by microscopic examination (p. 286).

The increased secretion and discharge of saliva, which occur on the introduction of food into the mouth, are due to *reflex* nervous action, the afferent or sensory filaments concerned being branches of the fifth cerebral and glossopharyngeal nerves, and the efferent fibres, the facial and sympathetic (Bernard). The chief nerve-centre concerned is situate in the medulla oblongata; but the submaxillary ganglion is also engaged, when the stimulus is other than gustatory (Bernard).

The influence of the nervous system on the secretion from the salivary glands has been made the subject of direct experiment on some of the lower animals, especially the dog; the submaxillary being the gland chiefly operated on, from the comparative facility with which it is exposed, with its vessels and nerves.

Nerve-fibres are supplied to the gland from the facial (chorda tympani), from the superior cervical ganglion of the sympathetic, and from the submaxillary ganglion. After exposure of the parts, if the *chorda tympani* be stimulated by a galvanic current, the arteries dilate, the stream of blood through the gland becomes larger and more rapid; even the veins may pulsate, and the blood in them is more arterial than venous. At the same time an abundance of watery saliva is secreted, and flows from the duct. A similar, but less striking effect is produced when the gustatory nerve

having been divided, its *central* end is galvanized. In this case, the stimulus conveyed to the medulla oblongata by the fibres of the gustatory is reflected to the submaxillary gland by the chorda tympani filaments of the facial. When, on the other hand, the stimulus is applied to the *sympathetic* filaments, the arteries contract, the blood stream is in consequence much diminished, and from the veins, when opened, there escapes only a sluggish stream of dark blood. The saliva, instead of being abundant and watery, becomes, as one would expect, scanty and tenacious. If both chorda tympani and sympathetic branches be divided, the gland, released from nervous control, secretes continuously and abundantly (*paralytic* secretion).

The abundant secretion of saliva, which follows stimulation of the chorda tympani, is not merely the result of a filtration of fluid from the blood-vessels, in consequence of the largely increased circulation through them. This is proved by the fact that, when the main duct is obstructed, the pressure within may considerably exceed the blood-pressure in the arteries (Ludwig). At the same time, the altered state of the blood-current is the chief factor, indirectly, in the production of the increased secretion, inasmuch as, with it, there is necessarily a greater supply of the materials, whence the gland-cells may take the constituents of saliva.

It is quite possible that the secreting cells are also directly influenced by the nervous system; and it may be fairly concluded that this is so, if Pflüger's observations on the termination of nerve-filaments in the cells (p. 286) are confirmed by future investigations.

The nerves which influence secretion in the parotid gland are branches of the facial (lesser superficial petrosal) and of the sympathetic. The former nerve, after passing through the otic ganglion, joins the auriculo-temporal branch of the fifth cerebral nerve, and, with it, is distributed to the gland. The nerves by which the stimulus exciting to secretion is conveyed to the medulla oblongata, are, as in the case of the submaxillary gland, the fifth, and the glossopharyngeal. The pneumogastric nerves convey a further stimulus to the secretion of saliva, when food has entered the stomach; the reflection occurring at the medulla oblongata.

The *purposes served by saliva* are of several kinds. In the first place, acting mechanically in conjunction with mucus, it keeps the mouth in a due condition of moisture, facilitating the movements of the tongue in speaking, and the mastication of food. (2.) It serves also in dissolving sapid substances, and rendering them capable of exciting the nerves of taste. But the principal mechanical purpose of the saliva is, (3) that by mixing with the food during mastication, it makes it a soft pulpy mass, such as may be easily swallowed. To this purpose the saliva is adapted both by quantity and quality. For, speaking generally, the quantity secreted during feeding is in direct proportion to the dryness and hardness of the food. The quality of saliva is equally adapted to this end. It is easy to see how much more

readily it mixes with most kinds of food than water alone does; and M. Bernard has shown that the saliva from the parotid, labial, and other small glands, being more aqueous than the rest, is that which is chiefly *braided* and mixed with the food in mastication; while the more viscid mucoid secretion of the submaxillary, palatine, and tonsillitic glands is spread over the surface of the softened mass, to enable it to slide more easily through the fauces and œsophagus. This view obtains confirmation from the interesting fact pointed out by Professor Owen, that in the great ant-eater, whose enormously elongated tongue is kept moist by a large quantity of viscid saliva, the submaxillary glands are remarkably developed, while the parotids are not of unusual size.

Beyond these, its mechanical purposes, saliva performs (4) a chemical part in the digestion of the food. When saliva, or a portion of a salivary gland, or even a portion of dried *ptyalin*, is added to starch paste in a test-tube and the mixture kept at a temperature of 100° F., the starch is very rapidly transformed into dextrin and grape-sugar.

In such an experiment the presence of sugar is at once discovered by the application of Trommer's test, which consists in the addition of a drop or two of a solution of sulphate of copper, followed by a larger quantity of caustic potash. When the liquid is boiled an orange red precipitate of suboxide of copper indicates the presence of sugar; and when common raw starch is masticated and mingled with saliva, and kept with it at a temperature of 90° or 100°, the starch-grains are cracked or eroded, and their contents are transformed in the same manner as the starch-paste.

Changes similar to these are effected on the starch of farinaceous food (especially after cooking) in the stomach; and it is reasonable to refer them to the action of the saliva, because the acid of the gastric fluid tends to retard or prevent, rather than favour, the transformation of the starch. It may therefore be held, that one purpose served by the saliva in the digestive process is that of assisting in the transformation of the starch, which enters so largely into the composition of most articles of vegetable food, and which (being naturally insoluble) is converted into soluble dextrin and grape-sugar, and made fit for absorption.

The power of converting starch into sugar appears in man to belong alike to the saliva secreted by the parotid, submaxillary, and sublingual glands, while in many of the lower animals, *e.g.*, dogs, it is only present in the parotid secretion.

The salivary glands of children do not become functionally active till the age of 4 to 6 months, and hence the bad effect of feeding them before this age on starchy food, corn flour, &c., which they are unable to render soluble and capable of absorption.

The important class of bodies, known as *Ferments*, exist chiefly in the digestive fluids. They are nitrogenous bodies, which have the power, under suitable conditions, of initiating and carrying on chemical changes in various organic substances; a very small quantity of the ferment serving for the transformation of very large quantities, *e.g.*, of starch into sugar or albuminoids into peptones (p. 307). They have, further, the following characters in common. Their action is retarded, or even quite prevented, by cold; a moderate warmth (100° F.) greatly facilitates it, while a high temperature (above 140° F.) completely prevents their action. In this case the action is not merely temporarily suspended, but irrecoverably destroyed. In many cases their action appears to depend upon taking up water: thus the transformation of starch, $C_6 H_{10} O_5$, into sugar, $C_6 H_{12} O$ involves the addition of one molecule of water, $C_6 H_{10} O_5 + H_2O = C_6 H_{12} O_6$. These ferments are termed "Hydrolytic." The chief classes of ferments are,—

1. *Sugar-forming, e.g., ptyalin, pancreatin.*
2. *Those which transform albuminoids into peptones; e.g., pepsin.*

Besides saliva, many azotised substances, especially if in a state of incipient decomposition, may excite the transformation of starch, such as pieces of the mucous membrane of the mouth, bladder, rectum, and other parts, various animal and vegetable tissues, and even morbid products; but the gastric fluid will not produce the same effect. The transformation in question is effected much more rapidly by saliva, however, than by any of the other fluids or substances experimented with, except the pancreatic secretion, which, as will be presently shown, is very analogous to saliva.

The majority of observers agree that the transformation of starch into sugar, on the entrance of the food into the stomach, is retarded, but not stopped. It is at least certain that the addition of a small quantity of hydrochloric acid (the strength of the acid being the same as that in the gastric juice) to a solution of starch and saliva does not stop the transformation into sugar.

Starch appears to be the only principle of food upon which saliva acts chemically: it has no apparent influence on any of the other ternary principles, such as sugar, gum, cellulose, or (according to Bernard) on fat, and seems to be equally destitute of power over albuminous and gelatinous substances.

The Pharynx.

That portion of the alimentary canal which intervenes between the mouth and the œsophagus is termed the *Pharynx* (fig. 134). It will suffice here to mention that it is constructed of a series of three muscles with striated fibres (*constrictors*), which are covered by a thin fascia externally, and are lined internally by a strong fascia (pharyngeal aponeurosis), on the inner aspect of which is areolar (submucous) tissue and mucous membrane, continuous with that of the mouth, and, in so far as the part concerned in swallowing is concerned, identical with it in general structure. The epithelium of this part of the pharynx, like that of the mouth, is laminated and squamous.

The pharynx is well supplied with mucous glands (Fig. 138).

The Tonsils.

Between the anterior and posterior arches of the soft palate are situated the *Tonsils*, one on each side. They consist essentially of masses of lymphoid tissue closely resembling Peyer's glands (p. 326), invested with a laminated epithelium. Their surface is indented by numerous depressions of various shapes (fig. 137), and into many of these crypts open the ducts of mucous glands (fig. 138), which are abundantly distributed through the proper adenoid or lymphoid tissue of the tonsils: here and there this lymphoid tissue comes right up to the free surface, replacing the usual epithelial investment.

Fig. 137.*

The viscid secretion which exudes from the tonsils may serve to lubricate the bolus of food as it passes them in the second part of the act of deglutition; and possibly the

* Fig. 137. Lingual follicle or crypt. *a*, Involution of mucous membrane with its papillæ; *b*, lymphoid tissue, with several lymphoid sacs (Frey).

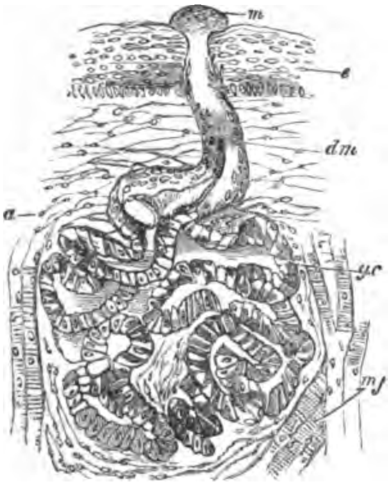
The tonsil is constructed essentially of a mass of follicles or crypts, more or less similar to the above, together with mucous glands, the ducts of which open into the bottom of the follicles.

lymphoid cells of the tonsils are the source of the so-called saliva-corpuscles.

Bodies similar to the tonsils have been described by Kölliker under the name of *pharyngeal tonsils:* they lie in the posterior part of the pharynx between the orifices of the Eustachian tubes.

(For the structure of *Mucous Glands*, see Chapter on Secretion.)

Fig. 138.*



The Œsophagus or Gullet.

The *Œsophagus* or Gullet (Fig. 134), the narrowest portion of the alimentary canal, is a muscular and mucous tube, nine or ten inches in length, which extends from the lower end of the pharynx to the cardiac orifice of the stomach. It is made up of three chief layers or *coats*—the outer *muscular*, the middle *areolar* or sub-mucous, and the innermost *mucous*.

The muscular coat, which is covered externally by connective tissue, consists of two layers of fibres—the outer being longitudinal, and the inner transverse. At the upper end of the œsophagus, the fibres of both these layers are, for the most part, *striated;* but, as we descend, the proportions of *striated* and *plain* fibres are gradually reversed, and only the latter are found in the lower half of the tube.

The mucous membrane, which, when the œsophagus is not distended, is thrown into numerous longitudinal folds or *rugæ*,

* Fig. 138. Mucous gland, from tongue of dog. *e*, epithelium, showing different shapes of nuclei at various depths; *m*, mucus discharged from orifice of *d m*, duct of mucous gland lined by epithelium, and containing a mass of mucus; *a*, areolar tissue of submucous layer; *m f*, muscular fibres of tongue; *g c*, gland cells of the various contorted tubes and acini of which the gland consists (Schofield).

is provided with minute *papillæ* and mucous glands (fig. 138). The former are buried beneath the thick laminated squamous epithelium, with which the tube is lined.

In newly-born children the mucous membrane exhibits, in many parts, the structure of lymphoid tissue (Klein.)

Between the mucous membrane and the submucous coat is a well-defined layer of plain muscular fibres (quite distinct from the layers, before mentioned, of the proper muscular coat), termed the *muscularis mucosæ.*

Blood- and lymph-vessels, and nerves, are distributed in the walls of the œsophagus. Between the outer and inner layers of the muscular coat, *ganglia* of Auerbach are also found.

Swallowing or Deglutition.

When properly masticated, the food is transmitted in successive portions to the stomach by the act of *deglutition* or *swallowing.* This act, for the purpose of description, may be divided into three parts. In the first, particles of food collected to a morsel glide between the surface of the tongue and the palatine arch, till they have passed the anterior arch of the fauces; in the second, the morsel is carried through the pharynx; and in the third, it reaches the stomach through the œsophagus. These three acts follow each other rapidly.

(1.) The first part of the act of deglutition may be voluntary, although it is usually performed unconsciously; the morsel of food, when sufficiently masticated, being pressed between the tongue and palate, by the agency of the muscles of the former, in such a manner as to force it back to the entrance of the pharynx.

(2.) The second act of deglutition is the most complicated, because the food must pass by the posterior orifice of the nose and the upper opening of the larynx without touching them. When it has been brought, by the first act, between the anterior arches of the palate, it is moved onwards by the tongue being carried backwards, and by the muscles of the anterior arches contracting on it and then behind it. The root of the tongue being retracted, and the larynx being raised with the pharynx and carried for-

wards under the tongue, the epiglottis is pressed over the upper opening of the larynx, and the morsel glides past it; the closure of the glottis being additionally secured by the simultaneous contraction of its own muscles: so that, even when the epiglottis is destroyed, there is little danger of food or drink passing into the larynx so long as its muscles can act freely. At the same time the raising of the soft palate, so that its posterior edge touches the back part of the pharynx, and the approximation of the sides of the posterior palatine arch, which move quickly inwards like side curtains, close the passage into the upper part of the pharynx and the posterior nares, and form an inclined plane, along the under surface of which the morsel descends; then the pharynx, raised up to receive it, in its turn contracts, and forces it onwards into the œsophagus.

(3.) In the third act, in which the food passes through the œsophagus, every part of that tube, as it receives the morsel and is dilated by it, is stimulated to contract: hence an undulatory contraction of the œsophagus, which is easily observable in horses while drinking, proceeds rapidly along the tube. It is only when the morsels swallowed are large, or taken too quickly in succession, that the progressive contraction of the œsophagus is slow, and attended with pain. Division of both pneumogastric nerves paralyses the contractile power of the œsophagus, and food accordingly accumulates in the tube (Bernard).

The second and third parts of the act of deglutition are involuntary.

The nerves engaged in the reflex act of deglutition are, mainly, sensory branches of the fifth cerebral, glosso-pharyngeal, and pneumo-gastric nerves; while the motor fibres concerned are branches of the fifth, the facial, the hypoglossal, the pneumogastric, and spinal accessory. The nerve-centre by which the muscles are harmonised in their action, is situate in the medulla oblongata. In the movements of the œsophagus, the ganglia contained in its walls, with the pneumo-gastrics, are the nerve-structures chiefly concerned.

It is important to note that the swallowing both of food and drink is a *muscular* act, and can, therefore, take place in opposi-

tion to the force of gravity. Thus, horses and many other animals habitually drink up-hill, and the same feat can be performed by jugglers.

DIGESTION OF FOOD IN THE STOMACH.

Structure of the Stomach.

In man and those Mammalia which are provided with a single stomach, its walls consist of four distinct layers or coats, viz., an external peritoneal, a muscular, a submucous, and a mucous coat; with blood-vessels, lymphatics, and nerves distributed in and between them.

The *peritoneal* coat has the structure of serous membranes in general. (See Serous Membranes.)

The *muscular coat* of the stomach consists of three separate layers or sets of fibres, which, according to their several directions, are named the longitudinal, circular, and oblique. The *longitudinal* set are the most superficial: they are continuous with the longitudinal fibres of the œsophagus, and spread out in a diverging manner over the great end and sides of the stomach. They extend as far as the pylorus, being especially distinct at the lesser or upper curvature of the stomach, along which they pass in several strong bands. The next set are the *circular* or *transverse* fibres, which more or less completely encircle all parts of the stomach; they are most abundant at the middle and in the pyloric portion of the organ, and form the chief part of the thick projecting ring of the pylorus. According to Pettigrew, these fibres are not simple circles, but form double or figure-of-8 loops, the fibres intersecting very obliquely. The next, and consequently deepest set of fibres, are the *oblique*, continuous with the circular muscular fibres of the œsophagus, and, according to Pettigrew, with the same double-looped arrangement that prevails in the preceding layer: they are comparatively few in number, and are placed only at the cardiac orifice and portion of the stomach, over both surfaces of which they are spread, some passing obliquely from left to right, others from right to left, around the cardiac orifice, to which, by their interlacing,

they form a kind of sphincter, continuous with that around the lower end of the œsophagus. The muscular fibres of the stomach and of the intestinal canal are *unstriped*, being composed of elongated, spindle-shaped fibre-cells. (See Section on Muscle.)

The *mucous membrane* of the stomach, which rests upon a layer of loose cellular membrane, or submucous tissue, is smooth, level, soft, and velvety; of a pale pink colour during life, and in the contracted state is thrown into numerous, chiefly longitudinal, folds or rugæ, which disappear when the organ is distended.

In its general structure the mucous membrane of the stomach resembles that of other parts. (See Structure of Mucous Membrane.) But there are certain peculiarities shared with the mucous membrane of the small and large intestines, which, doubtless, are connected with the peculiar functions, especially those relating to absorption, which these parts of the alimentary canal perform.

Entering largely into the construction of the mucous membrane, especially in the superficial part of the *corium*, is a quantity of a very delicate kind of connective tissue, called *retiform* tissue (fig. 147), or sometimes *lymphoid* or *adenoid* tissue, because it so closely resembles that which forms the stroma, or supporting framework of lymphatic glands (see Section on Lymphatic Glands); the resemblance being made much closer by the fact that the interspaces of this retiform tissue are filled with corpuscles not to be distinguished from lymph-corpuscles.

At the deepest part of the mucous membrane, is a layer of unstriped muscular fibres, called the *muscularis mucosæ* (fig. 140), which must not be confounded with the layers of muscle constituting the proper muscular coat, and from which it is separated by the submucous tissue.

When examined with a lens, the internal or free surface of the stomach presents a peculiar honeycomb appearance, produced by shallow polygonal depressions (fig. 139), the diameter of which varies generally from $\frac{1}{200}$th to $\frac{1}{350}$th of an inch; but near the pylorus is as much as $\frac{1}{100}$th of an inch. They are separated by slightly elevated ridges, which sometimes, especially in certain morbid states of the stomach, bear minute, narrow, vascular pro-

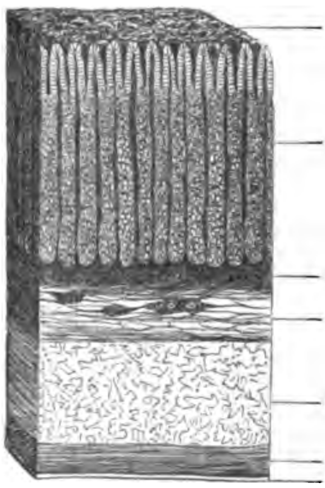
cesses, which look like villi, and have given rise to the erroneous supposition that the stomach has absorbing villi, like those of the small intestines. In the bottom of these little pits, and to some extent between them, minute openings are visible (fig. 139), which are the orifices of perpendicularly arranged tubular glands (fig. 140), imbedded side by side in sets or bundles, in the substance of the mucous membrane, and composing nearly the whole structure.

Fig. 139.*

The *glands* found in the human stomach may be divided into two classes, the *tubular* and *lenticular*.

Tubular glands.—The tubular glands may be escribed as a collection of cylinders with blind extremities, about $\frac{1}{85}$th of an

Fig. 140.†

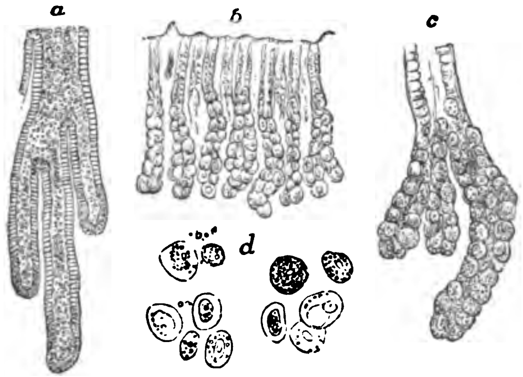


* Fig. 139. Small portion of the surface of the mucous membrane of the stomach. The specimen shows the shallow depressions, in each of which the smaller dark spots indicate the orifices of a variable number of the gastric tubular glands. × 30 (Ecker).

† Fig. 140. Portion of human stomach (magnified 30 diameters) cut vertically, both in a direction *parallel* to its long axis, and *across* it (altered from Brinton).

inch in length, and $\frac{1}{350}$th in diameter, packed closely together, with their long axis at right angles to the surface of the mucous membrane on which they open, their blind ends resting on the submucous tissue. (See fig. 140). They are all composed of basement membrane, and lined by epithelial cells, but they are not all of exactly similar shape; for while some are simple straight tubes, open at one end and closed at the other (fig. 141, *b*), others are at their deeper extremities branched (fig. 141, *c*).

Fig. 141.*



In the stomach of man, the simple undivided tubes are the rule, and the *branched* the exception (Brinton).

According to recent observations, three distinct kinds of cells may be distinguished in the peptic glands. (1) Ordinary columnar epithelium, which lines the upper fourth of the gland. (2) Smaller epithelial cells, approaching to a spheroidal form (these line the succeeding fourth of the tube, and also partly the lower end). (3) Large strongly granulated spheroidal 'peptic'

* Fig. 141. The gastric glands of the human stomach (magnified). *a*, deep part of a pyloric gastric gland (Kölliker); the cylindrical epithelium is traceable to the cæcal extremities. *b*, and *c*, cardiac gastric glands (Allen Thomson); *b*, vertical section of a small portion of the mucous membrane with the glands magnified 30 diameters; *c*, deeper portion of one of the glands, magnified 65 diameters, showing a slight division of the tubes, and a sacculated appearance, produced by the large glandular cells within them; *d*, cellular elements of the cardiac glands magnified 250 diameters.

cells, which form a continuous lining in some parts of the tube, while in other parts they are scattered irregularly, adhering to its outer part. They are readily distinguished by their large relative size and prominence. (See figs. 142 and 143.)

The peptic cells are especially prominent during digestion, while during fasting they are much less conspicuous, and the whole tubule appears shrunken (Heidenhain).

Fig. 142.*

In the greater number of the glands which are branched at their deeper extremities, the peptic and small spheroidal cells exist in the divisions, while the main duct and the upper part of the branches are lined by the cylindrical variety (fig. 141, *c*).

The varieties in the epithelial cells lining the different parts of the tubes, correspond probably with differences in the fluid secreted by their agency—the cylinder-epithelium, like that on the free surface of the stomach, being engaged in separating the thin alkaline mucus

Fig. 143.†

which is always present in greater or less quantity, while the larger glandular cells secrete the proper gastric juice.

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* Fig. 142. A gastric gland of cat in side view (Frey). *a*, cylindrical epithelium; *b*, small spheroidal epithelium; *c*, peptic cells; *d*, the part of the gland-tubules which is lined by two kinds of cells (peptic and small spheroidal).

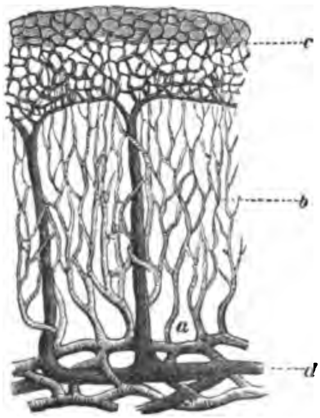
† Fig. 143. Transverse section through lower part of peptic glands of a cat (Frey). *a* peptic cells; *b*, small spheroidal cells; *c*, transverse section of capillaries.

Near the pylorus there exist glands branched at their deep extremities, which are lined throughout by cylinder-epithelium (fig. 141, *a*), and probably serve only for the secretion of mucus.

Lenticular glands.—Besides the cylindrical glands, there are also small closed lymphoid sacs beneath the surface of the mucous membrane, resembling exactly the *solitary* glands of the intestine, to be described hereafter. Their number is very variable, and they are found chiefly along the lesser curvature of the stomach, and in the pyloric region, but they may be present in any part of the organ. According to Dr. Brinton they are rarely absent in children. Their function doubtless resembles that of the intestinal solitary glands.

The blood-vessels of the stomach, which first break up in the submucous tissue, send branches upward between the closely packed glandular tubes, anastomosing around them by means of a fine capillary network with oblong meshes. Continuous with this deeper plexus, or prolonged upwards from it, so to speak, is a more superficial network of larger capillaries, which branch densely around the orifices of the tubes, and form the framework on which are moulded the small elevated ridges of mucous membrane bounding the minute, polygonal pits before referred to. From this *superficial* network the veins chiefly take their origin. Thence passing down between the tubes, with no very free connection with the deeper *inter-tubular*

Fig. 144.*



* Fig. 144. Plan of the bloodvessels of the stomach, as they would be seen in a vertical section. *a*, arteries, passing up from the vessels of sub-mucous coat; *b*, capillaries branching between and around the tubes; *c*, superficial plexus of capillaries occupying the ridges of the mucous membrane; *d*, vein formed by the union of veins which, having collected the blood of the superficial capillary plexus, are seen passing down between the tubes. (Brinton.)

capillary plexus, they open finally into the venous network in the submucous tissue.

The stomach possesses a highly developed lymphatic system, the radicles of which ascend between the tubules, nearly to the free surface, while large lymphatic sinuses exist in the submucous tissue.

The nerves of the stomach are derived from the pneumogastric and sympathetic, and form a plexus in the submucous and muscular coats, containing many ganglia (Remak, Meissner).

Secretion and Properties of the Gastric Fluid.

While the stomach contains no food, and is inactive, no gastric fluid is secreted; and mucus, which is either neutral or slightly alkaline, covers its surface. But immediately on the introduction of food or other substance into the stomach, the mucous membrane, previously quite pale, becomes slightly turgid and reddened with the influx of a larger quantity of blood; the gastric glands commence secreting actively, and an acid fluid is poured out in minute drops, which gradually run together and flow down the walls of the stomach, or soak into the substances introduced.

The first accurate analysis of the *gastric fluid* was made by Dr. Prout: but it does not appear that it was collected in any large quantity, or pure and separate from food, until the time when Dr. Beaumont was enabled, by a fortunate circumstance, to obtain it from the stomach of a man named St. Martin, in whom there existed, as the result of a gunshot wound, an opening leading directly into the stomach, near the upper extremity of the great curvature, and three inches from the cardiac orifice. The external opening was situate two inches below the left mamma, in a line drawn from that part to the spine of the left ilium. The borders of the opening into the stomach, which was of considerable size, had united, in healing, with the margins of the external wound, but the cavity of the stomach was at last separated from the exterior by a fold of mucous membrane, which projected from the upper and back part of the opening, and closed it like a valve, but could be pushed back with the finger. The introduction of any mechanical irritant, such as the bulb of a thermometer, into the stomach, excited at once the secretion of gastric fluid. This could be drawn off with a caoutchouc tube, and could often be obtained to the extent of nearly an ounce. The introduction of alimentary substances caused a much more rapid and abundant secretion of pure gastric fluid than the presence of other mechanical irritants did. No increase of temperature could be detected during the most active secretion; the thermometer introduced into the stomach always

stood at 100° Fahr., except during muscular exertion, when the temperature of the stomach, like that of other parts of the body, rose one or two degrees higher.

M. Blondlot, and subsequently M. Bernard, and several others, by maintaining fistulous openings into the stomachs of dogs, have confirmed most of the facts discovered by Dr. Beaumont. And the man St. Martin has frequently submitted to renewed experiments on his stomach, by various physiologists. From all these observations it appears, that pepper, salt, and other soluble stimulants, excite a more rapid discharge of gastric fluid than mechanical irritation does; so do alkalies generally, but acids have a contrary effect. When mechanical irritation is carried beyond certain limits so as to produce pain, the secretion, instead of being more abundant, diminishes or ceases entirely, and a ropy mucus is poured out instead. Very cold water, or small pieces of ice, at first render the mucous membrane pallid, but soon a kind of reaction ensues, the membrane becomes turgid with blood, and a larger quantity of gastric juice is poured out. The application of too much ice is attended by diminution in the quantity of fluid secreted, and by consequent retardation of the process of digestion. The quantity of the secretion seems to be influenced also by impressions made on the mouth; for Blondlot found that when sugar was introduced into the dog's stomach, either alone, or mixed with human saliva, a very small secretion ensued: but when the dog had himself masticated and swallowed it the secretion was abundant.

Dr. Beaumont described the secretion of the human stomach as "a clear transparent fluid, inodorous, a little saltish, and very perceptibly acid. Its taste is similar to that of thin mucilaginous water, slightly acidulated with muriatic acid. It is readily diffusible in water, wine, or spirits. It possesses the property of coagulating albumen in an eminent degree."

The chemical composition of the gastric juice of the human subject has been particularly investigated by Schmidt; a favourable case for his doing so occurring in the person of a peasant named Catherine Kütt, aged 35, who for three years had had a gastric fistula under the left mammary gland, between the cartilages of the ninth and tenth ribs.

The fluid was obtained by putting into the stomach some hard indigestible matter, as dry peas, and a little water, by which means the stomach was excited to secretion, at the same time that the matter introduced did not complicate the analysis by being digested in the fluid secreted. The gastric juice was drawn off through an elastic tube inserted into the fistula.

The fluid thus obtained was acid, limpid, and odourless, with

a mawkish taste. Its density varied from 1·0022 to 1·0024. Under the microscope a few cells from the gastric glands and some fine granular matter were observable.

The following table gives the mean of two analyses of the above-mentioned fluid; and arranged by the side of it, for purposes of comparison, is an analysis of gastric juice from the sheep and dog.

Composition of Gastric Juice.

		Human Gastric Juice.	Sheep's Gastric Juice.	Dog's Gastric Juice.
Water		994·40	986·14	971·17
Solid Constituents		5·59	13·85	28·82
Solids	Ferment, Pepsin (with a trace of Ammonia)	3.19	4·20	17·50
	Hydrochloric Acid	0·20	1·55	2·70
	Chloride of Calcium	0·06	0·11	1·66
	" Sodium	1·46	4.36	3·14
	" Potassium	0·55	1·51	1·07
	Phosphate of Calcium, Magnesium, and Iron	0.12	2·09	2·73

The *quantity* of gastric juice secreted daily has been variously estimated; but the average for a healthy adult may be assumed to range from ten to twenty pints in the twenty-four hours (Brinton).

Considerable difference of opinion has existed concerning the nature of the free acid contained in the gastric juice, chiefly whether it is *hydrochloric* or *lactic*. The weight of evidence, however, is in favour of free hydrochloric acid, being that to which, in the human subject, the acidity of the gastric fluid is mainly due; although there is no doubt that others, as lactic, acetic, butyric, are not unfrequently to be found therein.

Pepsin is a nitrogenous ferment (p. 291) which can be procured by digesting portions of the mucous membrane of the stomach in cold water, after they have been macerated for some time in water at a temperature between 80° and 100° F. The warm water dissolves various substances as well as some of the pepsin, but the cold water takes up little else than pepsin, which, on evaporating the cold solution, is obtained in a greyish-brown viscid fluid. The addition of alcohol throws down the pepsin in greyish-white flocculi.

Gastric Digestion.

The digestive power of the gastric juice depends on the pepsin and acid contained in it, both of which are necessary for the

process. Neither of them can digest alone; and when they are mixed, either the decomposition of the pepsin, or the neutralization of the acid at once destroys the digestive property of the fluid. The same fact is well shown by experimenting with an artificial gastric juice, prepared by dissolving pepsin in water, to which hydrochloric acid (1 part in 1000) has been added. A solution so made will digest portions of food placed in it if due precautions as to temperature be observed; while separate solutions of similar amounts of pepsin and hydrochloric acid respectively, are inert. For the perfection of the process of digestion, the following conditions are necessary; which are all present in the case of normal digestion—namely, (1) a temperature of about 100° F.; (2) such movements as the food is subjected to by the muscular contraction of the stomach, which bring in succession every part of it in contact with the mucous membrane, whence the fresh gastric juice is being secreted; (3) the constant removal of those portions which are already digested, so that what remains may be brought more completely into contact with the solvent fluid; and (4) a state of softness and minute subdivision, such as that to which the food is reduced by mastication before its introduction into the stomach.

The general effect of digestion in the stomach is the conversion of the food into *chyme*, a substance of various composition according to the nature of the food, yet always presenting a characteristic thick, pultaceous, grumous consistence, with the undigested portions of the food mixed in a more fluid substance, and a strong, disagreeable acid odour and taste.

Reduced into such a substance, all the various materials of a meal may be mingled together, and near the end of the digestive process hardly admit of recognition; but the experiments of artificial digestion, and the examination of stomachs with fistulæ, have illustrated many of the changes through which the chief alimentary principles pass, and the times and modes in which they are severally disposed of.

The functions of the gastric fluid may be, perhaps, best arranged under the following heads. (*a*) Its action on albu-

minous and other nitrogenous substances. (*b*) Its action on other varieties of food; and (*c*) as an antiseptic fluid.

The Action of Gastric Juice on Nitrogenous Food.

This is so well shown by Dr. Beaumont's experiments with human gastric juice, obtained from the man St. Martin, before referred to, that his account of one of them may be quoted. After the man had fasted seventeen hours, Dr. Beaumont took one ounce of gastric fluid, put into it a solid piece of boiled recently salted beef weighing three drachms, and placed the vessel which contained them in a water-bath heated to 100°. "In forty minutes digestion had distinctly commenced over the surface of the meat; in fifty minutes, the fluid had become quite opaque and cloudy, the external texture began to separate and become loose; and in sixty minutes chyme began to form. At 1 p.m." (two hours after the commencement of the experiment) "the cellular texture seemed to be entirely destroyed, leaving the muscular fibres loose and unconnected, floating about in small fine shreds, very tender and soft." In six hours, they were nearly all digested—a few fibres only remaining. After the lapse of ten hours, every part of the meat was completely digested. The gastric juice, which was at first transparent, was now about the colour of whey, and deposited a fine sediment of the colour of meat. A similar piece of beef was, at the time of the commencement of this experiment, suspended in the stomach by means of a thread: at the expiration of the first hour it was changed in about the same degree as the meat digested artificially; but at the end of the second hour, it was completely digested and gone.

Experiments showing the same facts, are easily performed with an artificial gastric fluid, obtained by macerating in water portions of the mucous membrane of a fresh stomach, and adding to the infusion a small quantity of hydrochloric acid.

"Open the stomach of a newly killed pig or rabbit, or the fourth stomach of a calf; remove its contents, and wash it thoroughly with a gentle stream of water without much rubbing. Lay it on a piece of board with its mucous surface upwards, fasten it down with a few pins, and then, with the back of a knife, or an ivory paper-cutter, scrape off all the mucus from the surface.

Rub it up in a mortar with clean silicious sand, or powdered glass, and water, let it stand some time, and then filter it. The filtrate is gastric juice in a state of very considerable purity. It is slightly opalescent, and contains a large quantity of pepsin and but little peptone. When acidulated with its own bulk of dilute hydrochloric acid of 0·2 per cent. it digests fibrin with great rapidity" (Brunton).

A very efficient way of preparing an artificial digestive fluid is to macerate small pieces of gastric mucous membrane in glycerine, which will take up large quantities of pepsin. An artificial gastric juice may be prepared, whenever it is wanted, by adding a little of the glycerine extract to dilute hydrochloric acid of 0·1 per cent.

Some albuminous foods, as the casein of milk, are coagulated by the action of the gastric fluid; and thus, before they are digested, come into the condition of the other solid principles of the food. Other albuminous solutions are not altered in this way; but all, solid or fluid, are changed in some of their chemical characters, before absorption.

The nature of the action by which pepsin and dilute acid effect a solution of albuminous substances is not well understood. Pepsin probably acts the part of a *hydrolytic* ferment (p. 291). The ultimate effect is the chemical modification of albuminous and gelatinous matters, in such a manner as to cause them to lose many of their most characteristic properties. To modifications of *albumen* the term *albuminose* or, more commonly, *peptone* is applied.

The main differences between *peptones* and ordinary albuminoid substances are:

1. They are *diffusible*.

2. They cannot be precipitated by heat, nitric, or acetic acid, or ferrocyanide of potassium. They are, however, thrown down by tannic acid, and by perchloride of mercury.

In the first-named quality peptones differ remarkably from albumen, and on its possession depends one of their chief uses. Albumen as such, even in a state of solution, would be of little service as food, inasmuch as its indiffusibility, or low endosmotic power, would effectually prevent its passing by absorption into the blood-vessels of the stomach and intestinal canal. Changed, however, by the action of the gastric juice into peptones, albuminous matters *diffuse* readily, and are thus quickly

X 2

absorbed. In other words, so far as their diffusibility is concerned, they have ceased to be *colloid*, and have in this respect become allied to the *crystalloids*.*

There are several modifications of peptone. Meissner describes three sorts which he distinguishes by the terms *a*, *b*, and *c* peptones; while other allied substances, also formed during digestion, have been named by the same authority *parapeptone*, *metapeptone*, and *dyspeptone*.

After entering the blood the peptones are very soon again modified, so as to re-assume the chemical characters of albumen, a change as necessary for preventing their diffusing out of the blood-vessels, as the previous change was for enabling them to pass in. This is effected, probably, in great part by the agency of the liver (p. 356).

(*b*) *The action of Gastric Juice on other than the Nitrogenous Constituents of the food.*

The *saccharine* and *amylaceous* principles are at first only mechanically separated from the vegetable substances within which they are contained, by the action of the gastric fluid. The soluble portions, viz., dextrin and sugar, are at once dissolved. The insoluble ones, viz. starch and lignin (or some parts of them) are rendered soluble and capable of absorption, by being converted into dextrin or grape-sugar. This change is carried on to some extent in the stomach; but the conversion of starch into sugar is effected, not by the gastric fluid, but by the saliva introduced with the food, or subsequently swallowed. The transformation of starch is continued in the intestinal canal, as will be shown, by the secretion of the pancreas, and perhaps by that of the intestinal glands. The power of digesting uncooked starch is, however, very limited in man and Carnivora; for when starch has been taken raw, as in corn and rice, large quantities of the granules are passed unaltered with the excrements. Cooking, by expanding or bursting the envelopes of the granules, renders their interior more amenable to the action of the digestive organs; and the abundant nutriment furnished by bread, and the large proportion that is absorbed of the weight consumed,

* These terms will be explained and illustrated in the Chapter on Absorption.

afford proof of the completeness of their power to make its starch soluble and prepare it for absorption.

Of the *oleaginous principles*,—as to their changes in the stomach, no more can be said than that they appear to be reduced to minute particles, and pass into the intestines mingled with the other constituents of the chyme. In the case of the solid fats, this effect is in great part produced by the solvent action of the gastric juice on the areolar tissue, albuminous cell-walls, etc., which enter into their composition, and by the solution of which the true fat is able to mingle more uniformly with the other constituents of the chyme.

The gastric fluid acts as a general solvent for some of the saline constituents of the food, as, for example, particles of common salt, which may happen to have escaped solution in the saliva; while its acid may enable it to dissolve some other salts which are insoluble in the latter or in water.

(*c*) *Antiseptic properties of the gastric fluid.*

That the secretions which the food meets with in the alimentary canal are antiseptic in their action, is what might be anticipated, not only from the proneness to decomposition of organic matters, such as those used as food, especially under the influence of warmth and moisture, but also from the well-known fact that decomposing flesh (*e.g.*, high game) may be eaten with impunity, while it would certainly cause disease and death were it allowed to enter the blood by any other route than that formed by the organs of digestion. The action, however, of the gastric juice in preventing and checking putrefaction has been often directly demonstrated. Dr. Beaumont observed that it was "powerfully antiseptic, checking the putrefaction of meats, and restorative of healthy action, when applied to old fœtid sores and foul ulcerating surfaces."

The details of two days' experiments performed by Dr. Beaumont on the man St. Martin, before referred to, may be here quoted :—

Exp. 42.—April 7th, 8 A.M. St. Martin breakfasted on three hard-boiled eggs, pancakes, and coffee. At half-past eight o'clock, Dr. Beaumont examined the stomach, and found a heterogeneous mixture of the several articles slightly digested. . . . . At a quarter past ten, no part of the breakfast remained in the stomach.

Exp. 43.—At eleven o'clock the same day, he ate two roasted eggs and

three ripe apples. In half an hour they were in an incipient state of digestion; and a quarter past twelve no vestige of them remained.

Exp. 44.—At two o'clock P.M. the same day, he dined on roasted pig and vegetables. At three o'clock they were half chymified, and at half-past four nothing remained but a very little gastric juice.

Again, Exp. 46.—April 9th. At three o'clock P.M. he dined on boiled dried codfish, potatoes, parsnips, bread, and butter. At half-past three o'clock examined, and took out a portion about half digested; the potatoes the least so. The fish was broken down into small filaments; the bread and parsnips were not to be distinguished. At four o'clock, examined another portion. Very few particles of fish remained entire. Some of the few potatoes were distinctly to be seen. At half-past four o'clock, he took out and examined another portion; all completely chymified. At five o'clock stomach empty.

Dr. Beaumont constructed a table showing the times required for the digestion of all usual articles of food in St. Martin's stomach, and in his gastric fluid taken from the stomach. Among the substances most quickly digested were rice and tripe, both of which were chymified in an hour; eggs, salmon, trout, apples, and venison, were digested in an hour and a half; tapioca, barley, milk, liver, fish, in two hours; turkey, lamb, potatoes, pig, in two hours and a half; beef and mutton required from three hours to three and a half, and both were more digestible than veal; fowls were like mutton in their degree of digestibility. Animal substances were, in general, converted into chyme more rapidly than vegetables.

Dr. Beaumont's experiments were all made on ordinary articles of food. A minuter examination of the changes produced by gastric digestion on various tissues has been made by Dr. Rawitz, who examined microscopically the product of the artificial digestion of different kinds of food, and the contents of the fæces after eating the same kinds of food.

The general results of the examinations, by Dr. Rawitz, as regards *animal* food, show that muscular tissue breaks up into its constituent fasciculi, and that these again are divided transversely; gradually the transverse striæ become indistinct, and then disappear; and finally, the sarcolemma seems to be dissolved, and no trace of the tissue can be found in the chyme, except a few fragments of fibres. These changes ensue most rapidly in the flesh of fish and hares, less rapidly in that of poultry and other animals. The cells of cartilage and fibro-cartilage, except those of fish, pass unchanged through the stomach and intestines, and may be found in the fæces. The interstitial tissues of these structures are converted into pulpy textureless substances in the artificial digestive fluid, and are not discoverable in the fæces. Elastic fibres are unchanged in the digestive fluid. Fat-cells are sometimes found quite unaltered in the fæces: and crystals of cholesterin may usually be obtained from fæces, especially after the use of pork fat.

As regards *vegetable* substances, Dr. Rawitz states, that he frequently found large quantities of cell-membranes unchanged in the fæces; also starch-cells, commonly deprived of only part of their contents. The green

colouring principle, chlorophyll, was usually unchanged. The walls of the sap-vessels and spiral vessels were quite unaltered by the digestive fluid, and were usually found in large quantities in the fæces; their contents, probably, were removed.

Under ordinary conditions, from three to four hours may be taken as the average time occupied by the digestion of a meal in the stomach. But many circumstances will modify the rate of gastric digestion. The chief are: the *nature* of the food taken and its *quantity* (the stomach should be fairly filled—not distended); the time that has elapsed since the last meal, which should be at least enough for the stomach to be quite clear of food; the amount of exercise previous and subsequent to a meal (gentle exercise being favourable, over-exertion injurious to digestion); the state of mind (tranquillity of temper being essential, in most cases, to a quick and due digestion); the bodily health; and some others.

Movements of the Stomach.

It has been already said, that the gastric fluid is assisted in accomplishing its share in digestion by the movements of the stomach. In granivorous birds, for example, the contraction of the strong muscular gizzard affords a necessary aid to digestion, by grinding and triturating the hard seeds which constitute part of the food. But in the stomachs of man and Mammalia the motions of the muscular coat are too feeble to exercise any such mechanical force on the food; neither are they needed, for mastication has already done the mechanical work of a gizzard; and the experiments of Réaumur and Spallanzani have demonstrated that substances enclosed in perforated tubes, and consequently protected from mechanical influence, are yet digested.

The normal actions of the muscular fibres of the human stomach appear to have a three-fold purpose; (1) to adapt the stomach to the quantity of food in it, so that its walls may be in contact with the food on all sides, and, at the same time, may exercise a certain amount of compression upon it; (2) to keep the orifices of the stomach closed until the food is digested; and (3) to perform certain peristaltic movements, whereby the food,

as it becomes chymified, is gradually propelled towards, and ultimately through, the pylorus. In accomplishing this latter end, the movements without doubt materially contribute towards effecting a thorough intermingling of the food and the gastric fluid.

When digestion is not going on, the stomach is uniformly contracted, its orifices not more firmly than the rest of its walls; but, if examined shortly after the introduction of food, it is found closely encircling its contents, and its orifices are firmly closed like sphincters. The cardiac orifice, every time food is swallowed, opens to admit its passage to the stomach, and immediately again closes. The pyloric orifice, during the first part of gastric digestion, is usually so completely closed, that even when the stomach is separated from the intestines, none of its contents escape. But towards the termination of the digestive process, the pylorus seems to offer less resistance to the passage of substances from the stomach; first it yields to allow the successively digested portions to go through it; and then it allows the transit of even undigested substances.

From the observations of Dr. Beaumont on the man St. Martin, it appears that food, so soon as it enters the stomach, is subjected to a kind of peristaltic action of the muscular coat, whereby the digested portions are gradually approximated towards the pylorus. The movements were observed to increase in rapidity as the process of chymification advanced, and were continued until it was completed.

The contraction of the fibres situated towards the pyloric end of the stomach seems to be more energetic and more decidedly peristaltic than those of the cardiac portion. Thus, Dr. Beaumont found that when the bulb of the thermometer was placed about three inches from the pylorus, it was tightly embraced from time to time, and drawn towards the pyloric orifice for a distance of three or four inches. The object of this movement appears to be, as just said, to carry the food towards the pylorus as fast as it is formed into chyme, and to propel the chyme into the duodenum; the undigested portions of food being kept back until they are also reduced into chyme, or until all that is

digestible has passed out. The action of these fibres is often seen in the contracted state of the pyloric portion of the stomach after death, when it alone is contracted and firm, while the cardiac portion forms a dilated sac. Sometimes, by a predominant action of strong circular fibres placed between the cardia and pylorus, the two portions, or ends as they are called, of the stomach, are separated from each other by a kind of hour-glass contraction.

The interesting researches of Dr. Brinton have clearly established that, by means of this peristaltic action of the muscular coats of the stomach, not merely is chymified food gradually propelled through the pylorus, but a kind of double current is continually kept up among the contents of the stomach, the circumferential parts of the mass being gradually moved onward towards the pylorus by the peristaltic contraction of the muscular fibres, while the central portions are propelled in the opposite direction, namely, towards the cardiac orifice; in this way is kept up a constant circulation of the contents of the viscus, highly conducive to their free mixture with the gastric fluid and to their ready digestion.

Vomiting.

The mechanism by which the act of vomiting is effected will be best understood by referring to a former chapter in which various respiratory actions are considered (p. 252). The expulsion of the contents of the stomach in vomiting, like that of mucus or other matter from the lungs in *coughing*, is preceded by an inspiration; the glottis is then closed, and immediately afterwards the abdominal muscles strongly act; but here occurs the difference in the two actions. Instead of the vocal cords yielding to the action of the abdominal muscles, they remain tightly closed. Thus the diaphragm being unable to go up, forms an unyielding surface against which the stomach can be pressed. It is *fixed*, to use a technical phrase. At the same time the *cardiac* sphincter-muscle being relaxed, and the orifice which it naturally guards being actively dilated, while the *pylorus* is closed, and the stomach itself also contracting, the action of the

abdominal muscles, by these means assisted, expels the contents of the organ through the œsophagus, pharynx, and mouth. The reversed peristaltic action of the œsophagus probably increases the effect.

It has been frequently stated that the stomach itself is quite passive during vomiting, and that the expulsion of its contents is effected solely by the pressure exerted upon it when the capacity of the abdomen is diminished by the contraction of the diaphragm, and subsequently of the abdominal muscles. The experiments and observations, however, which are supposed to confirm this statement, only show that the contraction of the abdominal muscles alone is sufficient to expel matters from an unresisting bag through the œsophagus; and that, under very abnormal circumstances, the stomach, by itself, cannot expel its contents. They by no means show that in ordinary vomiting the stomach is passive; and, on the other hand, there are good reasons for believing the contrary.

It is true that facts are wanting to demonstrate with certainty this action of the stomach in vomiting; but some of the cases of fistulous opening into the organ appear to support the belief that it does take place; * and the analogy of the case of the stomach with that of the other hollow viscera, as the rectum and bladder, may be also cited in confirmation.

Besides the influence which it may thus have by its contraction, the stomach also essentially contributes to the act of vomiting, by the contraction of its pyloric orifice at the same time that the oblique fibres around the cardiac orifice are relaxed. For, until the relaxation of these fibres, no vomiting can ensue; when contracted, they can as well resist all the force of the contracting abdominal and other muscles, as the muscles by which the glottis is closed can resist the same force in the act of straining. Doubtless we may refer many of the acts of retching and ineffectual attempts to vomit, to the want of concord between the relaxation of these muscles and the contraction of the others.

The muscles which contract during vomiting, are chiefly and primarily those of the abdomen; the diaphragm also acts, but usually not as the muscles of the abdominal walls do. They contract and compress the stomach more and more towards the back and upper parts of the diaphragm; and the diaphragm (which is usually drawn down in the deep inspiration that precedes each act of vomiting) is fixed, and presents an unyielding surface against which the stomach may be pressed. The diaphragm is, therefore, as a rule passive, during the actual expulsion of the contents of the stomach. But there are grounds

* A collection of cases of fistulous communication with the stomach, through the abdominal parietes, has been given by Dr. Murchison, in vol. xli. of the Medico-Chirurgical Transactions.

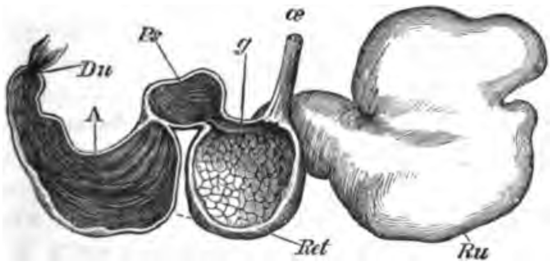
for believing that sometimes this muscle actively contracts, so that the stomach is, so to speak, squeezed between the descending diaphragm and the retracting abdominal walls (fig. 133).

Some persons possess the power of vomiting at will, without applying any undue irritation to the stomach, but simply by a voluntary effort. It seems also, that this power may be acquired by those who do not naturally possess it, and by continual practice may become a habit. There are cases also of rare occurrence in which persons habitually swallow their food hastily, and nearly unmasticated, and then at their leisure regurgitate it, piece by piece, into their mouth, remasticate, and again swallow it, like members of the ruminant order of Mammalia.

The nerve-actions concerned in vomiting are probably governed by a nerve-centre situate in the medulla oblongata.

The *Ruminants* (ox, sheep, deer, &c.) possess very complex stomachs; in most of them four distinct cavities are to be distinguished (Fig. 145).

Fig. 145.*



1. The *Paunch*, or *Rumen*, a very large cavity which occupies the cardiac end of the stomach, and into which large quantities of food are in the first instance swallowed with little or no mastication.

2. The *Reticulum*, or *Honeycomb* stomach, so called from the fact that its mucous membrane is disposed in a number of folds enclosing hexagonal cells.

3. The *Psalterium*, or *Manyplies*, in which the mucous membrane is arranged in very prominent longitudinal folds.

4. *Abomasum*, *Reed* or *Rennet*, which is narrow and elongated, its mucous membrane being much more highly vascular than that of the other divisions.

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* Fig. 145. Stomach of sheep. *œ.* Œsophagus; *Ru.* Rumen; *Ret.* Reticulum; *Ps.* Psalterium or Manyplies; *A.* Abomasum; *Du.* Duodenum; *g.* Groove from œsophagus to psalterium (Huxley).

In the process of rumination small portions of the contents of the rumen and reticulum are successively regurgitated into the mouth, and there thoroughly masticated and insalivated (chewing the cud): they are then again swallowed, being this time directed by a groove (which in the figure is seen running from the lower end of the œsophagus) into the manyplies, and thence into the abomasum.

It will thus be seen that the first two stomachs (paunch and reticulum) have chiefly the mechanical functions of storing and moistening the fodder; the third (manyplies) probably acts as a strainer, only allowing the finely divided portions of food to pass on into the fourth stomach, where the gastric juice is secreted and the process of digestion carried on. The mucous membrane of the first three stomachs is lowly vascular, while that of the fourth is pulpy, glandular, and highly vascular.

In some other animals, as the pig, a similar distinction obtains between the mucous membrane in different parts of the stomach.

In the pig the glands in the cardiac end are few and small, while towards the pylorus they are abundant and large.

A similar division of the stomach into a cardiac (receptive) and a pyloric (digestive) part, foreshadowing the complex stomach of ruminants, is seen in the common rat, in which these two divisions of the stomach are distinguished, not only by the characters of their lining membrane, but also by a well-marked constriction.

In birds the function of mastication is performed by the stomach (gizzard) which in granivorous orders, *e.g.* the common fowl, possesses very powerful muscular walls and a dense horny epithelium.

Hunger and Thirst.

The sensation of *hunger* is manifested in consequence of deficiency of food in the system. The mind refers the sensation to the stomach; yet since the sensation is relieved by the introduction of food either into the stomach itself, or into the blood through other channels than the stomach, it would appear not to depend on the state of the stomach alone. This view is confirmed by the fact, that the division of both pneumogastric nerves, which are the principal channels by which the mind is cognisant of the condition of the stomach, does not appear to allay the sensations of hunger.

But that the stomach has some share in this sensation is proved by the relief afforded, though only temporarily, by the introduction of even non-alimentary substances into this organ. It may, therefore, be said that the sensation of hunger is derived from the system generally, but chiefly from the condition of the stomach, the nerves of which, we may suppose, are more affected

by the state of the insufficiently replenished blood than those of other organs are.

The sensation of *thirst*, indicating the want of fluid, is referred to the fauces, although, as in hunger, this is merely the local declaration of a general condition. For thirst is relieved for only a very short time by moistening the dry fauces; but may be relieved completely by the introduction of liquids into the blood, either through the stomach, or by injections into the blood-vessels, or by absorption from the surface of the skin or the intestines. The sensation of thirst is perceived most naturally whenever there is a disproportionately small quantity of water in the blood: as well, therefore, when water has been abstracted from the blood, as when saline or any solid matters have been abundantly added to it. We can express the fact (even if it be not an explanation of it), by saying that the nerves of the mouth and fauces, through which the sense of thirst is chiefly derived, are more sensitive to this condition of the blood than other nerves are. And the cases of hunger and thirst are not the only ones in which the mind derives, from certain organs, a peculiar predominant sensation of some condition affecting the whole body. Thus, the sensation of the "necessity of breathing," is referred especially to the lungs; but, as Volkmann's experiments show, it depends on the condition of the blood which circulates everywhere, and is felt even after the lungs of animals are removed; for they continue, even then, to gasp and manifest the sensation of want of breath. And, as with respiration when the lungs are removed, the mind may still feel the body's want of breath; so in hunger and thirst, even when the stomach has been filled with innutritious substances, or the pneumogastric nerves have been divided, and the mouth and fauces are kept moist, the mind is still aware, by the more obscure sensations in other parts, of the whole body's need of food and water.

Influence of the Nervous System on Gastric Digestion.

The normal movements of the stomach during gastric digestion are directly connected with the plexus of nerves and ganglia

contained in its walls (p. 302), the presence of food acting as a stimulus which is conveyed to the ganglia and reflected to the muscular fibres. The stomach is, however, also directly connected with the higher nerve-centres by means of branches of the vagus and solar plexus of the sympathetic. The vasomotor fibres of the latter are derived, probably, from the splanchnic nerves.

The special function of the pneumogastric nerves in connection with the movements of the stomach is not certainly known. Irritation of the vagi produces contraction of the stomach, if digestion is proceeding; while, on the other hand, its peristaltic action is retarded or stopped, when these nerves are divided.

The *influence of the nervous system on the secretion of gastric fluid*, is shown plainly enough in the influence of the mind upon digestion in the stomach; and is, in this regard, well illustrated by several of Dr. Beaumont's observations. M. Bernard also, watching the act of gastric digestion in dogs which had fistulous openings into their stomachs, saw that on the instant of dividing their pneumogastric nerves, the process of digestion was stopped, and the mucous membrane of the stomach, previously turgid with blood, became pale, and ceased to secrete. These facts may be explained by the theory that the pneumogastric nerves are the media by which, during digestion, an *inhibitory* impulse is conducted to the vaso-motor centre in the medulla; such impulse being reflected along the splanchnic nerves to the blood-vessels of the stomach, and causing their dilatation (Rutherford). From other experiments it may be gathered, that although, as in M. Bernard's, the division of both pneumogastric nerves always temporarily suspends the secretion of gastric fluid, and so arrests the process of digestion, and is occasionally followed by death from inanition; yet the digestive powers of the stomach may be completely restored after the operation, and the formation of chyme and the nutrition of the animal may be carried on almost as perfectly as in health.

M. Bernard found that galvanic stimulus of these nerves excited an active secretion of the fluid, while a like stimulus applied to the sympathetic nerves issuing from the semilunar

ganglia, caused a diminution and even complete arrest of the secretion.

In thirty experiments on Mammalia, which M. Wernscheidt performed under Müller's direction, not the least difference could be perceived in the action of narcotic poisons introduced into the stomach, whether the pneumogastric had been divided on both sides or not, provided the animals were of the same species and size. It appears, however, that such poisons as are capable of being rendered inert by the action of the gastric fluid, may, if taken into the stomach shortly after division of both pneumogastric nerves, produce their poisonous effects; in consequence, apparently, of the temporary suspension of the secretion of gastric fluid. Thus, in one of his experiments, M. Bernard gave to each of two dogs, in one of which he had divided the pneumogastric nerves, a dose of emulsine, and half an hour afterwards a dose of amygdaline, substances which are innocent alone, but when mixed produce hydrocyanic acid. The dog whose nerves were cut, died in a quarter of an hour, the substances being absorbed unaltered and mixing in the blood; in the other, the emulsine was decomposed by the gastric fluid before the amygdaline was administered; therefore, hydrocyanic acid was not formed in the blood, and the dog survived.

Digestion of the Stomach after Death.

If an animal die during the process of gastric digestion, and when, therefore, a quantity of gastric juice is present in the interior of the stomach, the walls of this organ itself are frequently themselves acted on by their own secretion, and to such an extent, that a perforation of considerable size may be produced, and the contents of the stomach may in part escape into the cavity of the abdomen. This phenomenon is not unfrequently observed in *post-mortem* examinations of the human body; but, as Dr. Pavy observes, the effect may be rendered, by experiment, more strikingly manifest. "If, for instance," he remarks, "an animal, as a rabbit, be killed at a period of digestion, and afterwards exposed to artificial warmth to prevent its temperature from falling, not only the stomach, but many of the surrounding parts will be found to have been dissolved. With a rabbit killed in the evening, and placed in a warm situation (100° to 110° Fahr.) during the night, I have seen in the morning, the stomach, diaphragm, part of the liver and lungs, and the intercostal muscles of the side upon which the animal was laid all digested away, with the muscles and skin of the neck and upper extremity on the same side also in a semi-digested state."

From these facts, it becomes an interesting question why, during life, the stomach is free from liability to injury from a secretion, which, after death, is capable of such destructive effects? John Hunter, who particularly drew attention to the phenomena of *post-mortem* digestion, explained the immunity from injury of the living stomach, by referring it to the protective influence of the "vital principle." But this dictum has been called in question by subsequent observers. It is, indeed, rather a statement of a fact, than an explanation of its cause. It must be confessed, however, that no entirely satisfactory theory has been yet stated as a substitute.

It is only necessary to refer to the idea of Bernard, that the living stomach finds protection from its secretion in the presence of epithelium and mucus, which are constantly renewed in the same degree that they are constantly dissolved, in order to remark that this theory, so far, at least, as the epithelium is concerned, has been disproved by experiments of Pavy's, in which the mucous membrane of the stomachs of dogs was dissected off for a small space, and, on killing the animals some days afterwards, no sign of digestion of the stomach was visible. "Upon one occasion, after removing the mucous membrane and exposing the muscular fibres over a space of about an inch and a half in diameter, the animal was allowed to live for ten days. It ate food every day, and seemed scarcely affected by the operation. Life was destroyed whilst digestion was being carried on, and the lesion in the stomach was found very nearly repaired: new matter had been deposited in the place of what had been removed, and the denuded spot had contracted to much less than its original dimensions."

Dr. Pavy believes that the natural alkalinity of the blood, which circulates so freely during life in the walls of the stomach, is sufficient to neutralize the acidity of the gastric juice; and as may be gathered from what has been previously said (p. 304-5), the neutralization of the acidity of the gastric secretion is quite sufficient to destroy its digestive powers. He also very ingeniously argues that this very alkalinity must, from the conditions of the circulation naturally existing in the walls of the stomach,

be increased in proportion to the need of its protective influence. "In the arrangement of the vascular supply," he remarks, "a doubly effective barrier is, as it were, provided. The vessels pass from below upwards towards the surface: capillaries having this direction ramify between the tubules by which the acid of the gastric juice is secreted; and being separated by secretion below, must leave the blood that is proceeding upwards correspondingly increased in alkalinity; and thus, at the period when the largest amount of acid is flowing into the stomach, and the greatest protection is required, then is the provision afforded in its highest state of efficiency."

Dr. Pavy's theory is the best and most ingenious hitherto framed in connection with this subject; but the experiments adduced in its favour are open to many objections, and afford only a negative support to the conclusions they are intended to prove. The matter, therefore, can scarcely be considered finally settled.

DIGESTION IN THE INTESTINES.

The Intestinal Canal is divided into two chief portions, named, from their differences in diameter, the *small* and *large* intestine (fig. 134). These are continuous with each other, and communicate by means of an opening guarded by a valve, the *ileo-cæcal valve*, which allows the passage of the products of digestion from the small into the large bowel, but not, under ordinary circumstances, in the opposite direction.

The structure and functions of each organ or tissue concerned in intestinal digestion will be first described in detail, and afterwards a summary will be given of the changes which the food undergoes in its passage through the intestines, 1st, from the pylorus to the ileo-cæcal valve; and, 2nd, from the ileo-cæcal valve to the anus.

Structure and Secretions of the Small Intestine.

The Small Intestine, the average length of which in an adult is about twenty feet, has been divided, for convenience of description, into three portions, viz., the *duodenum*, which ex-

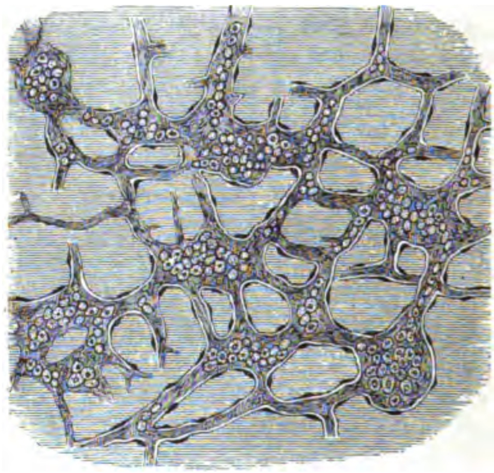
tends for eight or ten inches beyond the pylorus; the *jejunum*, which occupies two-fifths, and the *ileum*, which occupies three-fifths of the rest of the canal.

The small intestine, like the stomach, is constructed of four principal coats, viz., the serous, muscular, sub-mucous, and mucous.

(1). The *serous* coat, formed by the visceral layer of the peritoneum, need not be here specially described. It has the structure of serous membranes in general.

(2). The *muscular* coats consist of an internal circular and an

Fig. 146.*



external longitudinal layer: the former is usually considerably the thicker. Both alike consist of bundles of unstriped muscular tissue supported by connective tissue. They are well provided with lymphatic vessels, which form a set distinct from those of the mucous membrane.

* Fig. 146. Auerbach's nerve-plexus in small intestine. The plexus consists of fibrillated substance, and is made up of trabeculæ of various thicknesses. Nucleus-like elements (unformed ganglion-cells) and ganglion-cells are imbedded in the plexus, the whole of which is enclosed in a nucleated sheath (Klein).

Between the two muscular coats is a nerve plexus (Auerbach's plexus, plexus myentericus) (fig. 146) similar in structure to Meissner's (in the sub-mucous tissue), but with more numerous ganglia. There can be little doubt that this plexus regulates the peristaltic movements of the muscular coats of the intestines.

(3). Between the mucous and muscular coats, is the *submucous* coat, which consists of areolar tissue, in which numerous blood-vessels and lymphatics ramify. A fine plexus, consisting mainly of non-medullated nerve-fibres, "Meissner's plexus," with ganglion cells at its nodes, occurs in the submucous tissue from the stomach to the anus. From the position of this plexus and the distribution of its branches, it seems highly probable that it is the local centre for regulating the calibre of the blood-vessels supplying the intestinal mucous membrane, and presiding over the processes of secretion and absorption.

Fig. 147.*

(4). The *mucous membrane* is the most important coat in relation to the function of digestion. The following structures which enter into its composition may be now successively described;—the *valvulæ conniventes;* the *villi;* and the *glands.* The general structure of the mucous membrane of the intestines resembles that of the stomach (p. 297), and, like it, is lined on its inner surface by columnar epithelium. *Lymphoid* or *Retiform* tissue (fig. 147) enters largely into its construction; and on its deep surface is a layer of the *muscularis mucosæ* (*m*, fig. 154).

* Fig. 147. The figure represents a cross section of a small fragment of the mucous membrane, including one entire crypt of Lieberkühn and parts of several others: *a*, cavity of the tubular glands or crypts; *b*, one of the lining epithelial cells; *c*, the lymphoid or retiform spaces, of which some are empty, and others occupied by lymph cells, as at *d*.

Valvulæ Conniventes.—The *valvulæ conniventes* (fig. 148) commence in the duodenum, about one or two inches beyond the pylorus, and becoming larger and more numerous immediately beyond the entrance of the bile-duct, continue thickly arranged and well developed throughout the jejunum; then, gradually diminishing in size and number, they cease near the middle of the ileum. They are formed by a doubling inwards of the mucous membrane; the crescentic, nearly circular, folds thus formed being arranged transversely to the axis of the intestine, and each individual fold seldom extending around more than $\frac{1}{2}$ or $\frac{2}{3}$ of the bowel's circumference. Unlike the rugæ in the œsophagus and stomach, they do not disappear on distension of the canal. Only an imperfect notion of their natural position and function can be obtained by looking at them after the intestine has been laid open in the usual manner. To understand them aright, a piece of gut should be distended either with air or alcohol, and not opened until the tissues have become hardened. On then making a section, it will be seen that instead of disappearing, they stand out at right angles to the general surface of the mucous membrane (fig. 148). Their functions are probably these—Besides (1) offering a largely increased surface for secretion and absorption, they probably (2) prevent the too rapid passage of the very liquid products of gastric digestion, immediately after their escape from the stomach, and (3), by their projection, and consequent interference with an uniform and untroubled current of the intestinal contents, probably assist in the more perfect mingling of the latter with the secretions poured out to act on them.

Fig. 148.*

Glands of the Small Intestine.—The glands are of three prin-

* Fig. 148. Piece of small intestine (previously distended and hardened by alcohol) laid open to show the normal position of the valvulæ conniventes.

cipal kinds, named after their describers, the glands of Lieberkühn, of Peyer, and of Brunn.

The *glands* or *follicles of Lieberkühn* are simple tubular depressions of the intestinal mucous membrane, thickly distributed over the whole surface both of the large and small intestines. In the small intestine they are visible only with the aid of a lens; and their orifices appear as minute dots scattered between the villi. They are larger in the large intestine, and increase in size the nearer they approach the anal end of the intestinal tube; and in the rectum their orifices may be visible to the naked eye. In length they vary from $\frac{1}{30}$ to $\frac{1}{10}$ of a line. Each tubule (fig. 150) is constructed of the same essential parts as the intestinal mucous membrane, viz., a fine structureless *membrana propria*, or basement membrane, a layer of cylindrical epithelium lining it, and capillary blood-vessels covering its exterior. Their contents appear to vary, even in health; the varieties being dependent, probably, on the period of time in relation to digestion at which they are examined. In the columnar epithelium of Lieberkühn's follicles, goblet-cells frequently occur; the free surface of the cells presenting an appearance precisely similar to the "striated basilar border" which covers the villi. The purpose served by the material secreted by these glands is still doubtful. Their large number and the extent of surface occupied by them, seem, however, to indicate that they are concerned in other and higher offices (p. 337) than the mere production of mucus to

Fig. 149.*

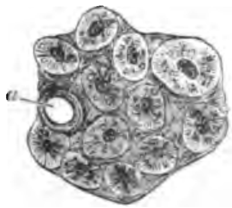


Fig. 150.†

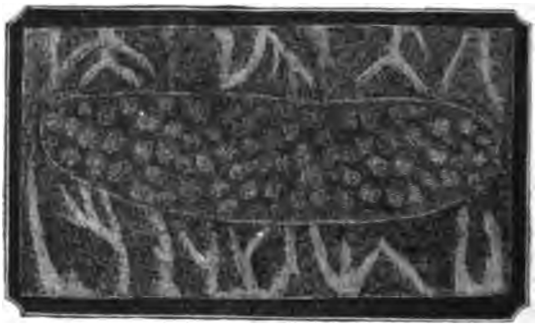
* Fig. 149. Openings of the glands of Lieberkühn in the small intestine of the mouse. At *a*, is an empty opening; in the other cases each is filled with columnar epithelial cells (Frey).

† Fig. 150. A gland of Lieberkühn, in longitudinal section (Brinton).

moisten the surface of the mucous membrane, although, doubtless, this is one of their functions.

The *glands of Peyer* occur chiefly but not exclusively in the *small* intestine. They are found in greatest abundance in the lower part of the ileum near to the ileo-cæcal valve. They are met with in two conditions, viz., either scattered singly, in which case they are termed *glandulæ solitariæ*, or aggregated in groups varying from one to three inches in length and about half-an-inch in width, chiefly of an oval form, their long axis parallel with that of the intestine. In this state, they are named *glandulæ*

Fig. 151.*



agminatæ, the groups being commonly called *Peyer's patches* (fig. 151). The latter are placed almost always opposite the attachment of the mesentery. In structure, and probably in function, there is no essential difference between the solitary glands and the individual bodies of which each group or patch is made up; but the surface of the solitary glands (fig. 152) is beset with villi, from which those forming the agminate patches (fig. 153), are usually free. In the condition in which they have been most commonly examined, each gland appears as a circular opaque-white sacculus, from half a line to a line in diameter, and, according to the degree in which it is developed, either

* Fig. 151. Agminate follicles, or *Peyer's patch*, in a state of distension, magnified about 5 diameters (Boehm).

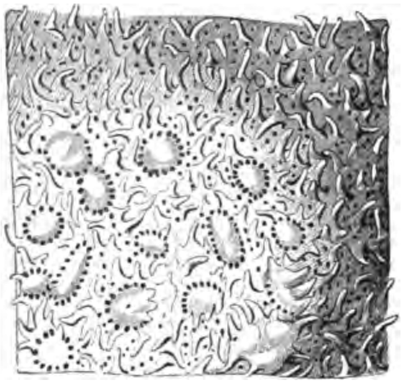
sunk beneath, or more or less prominently raised on, the surface of a depression or fossa in the mucous membrane. Each gland is surrounded by the openings of Lieberkühn's follicles (fig. 153).

When viewed in a vertical section of the mucous membrane, Peyer's glands appear of an ovoid form, their base being imbedded in the submucous tissue, while their apices project more or less on the free surface of the mucous membrane (*a*, fig. 155).

They consist essentially of adenoid or retiform tissue *i.e.*, a delicate supporting stroma of reticular connective tissue in the interstices of which lymphoid corpuscles are closely packed.

Fig. 152.*

Fig. 153.†



The adjacent glands of a Peyer's patch are connected together by similar tissue.

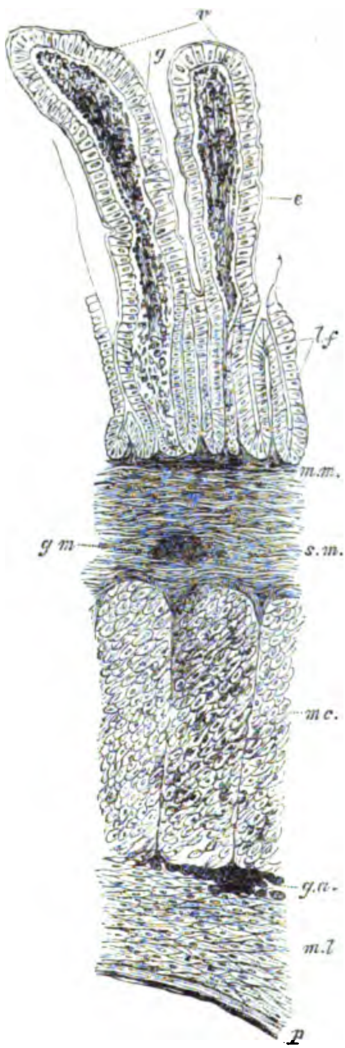
The surface projecting into the intestine is usually covered by columnar epithelium, but often the lymphoid tissue comes right up to the free surface, replacing the epithelium as is the case in the tonsil (p. 292).

* Fig. 152. Solitary gland of small intestine (Boehm).

† Fig. 153. Part of a patch of the so-called Peyer's glands magnified, showing the various forms of the sacculi, with their zone of foramina. The rest of the membrane marked with Lieberkühn's follicles, and sprinkled with villi (Boehm).

Peyer's glands are surrounded by lymphatic sinuses which do not penetrate into their interior; the interior is, however, traversed by a very rich blood capillary plexus. If the vermiform appendix of a rabbit which consists of a mass of Peyer's glands be injected with blue by pressing the point of a fine syringe into one of the lymphatic sinuses, the Peyer's glands will appear as greyish white spaces surrounded by blue; if now the arteries of the same be injected with red, the greyish patches will change to red, thus proving that they are *surrounded* by lymphatic spaces but *penetrated* by blood-vessels. The lacteals passing out of the villi communicate with the lymph sinuses round Peyer's glands.

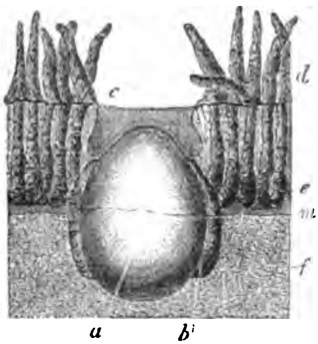
Fig. 154.*



* Fig. 154. Vertical longitudinal section through small intestine of dog, showing the structure and relative position of the several layers; *v.* two villi showing *e*, epithelium; *g*, goblet cells. The free surface is seen to be formed by the "striated basilar border," while inside the villus the adenoid tissue and unstriped muscle-cells are seen; *lf*, Lieberkühn's follicles; *mm*, muscularis mucosæ, sending up fibres between the follicles into the villi; *sm*, submucous tissue; containing (*gm*), ganglion cells of Meissner's plexus; *mc*, circular muscular coat of great thickness, with connective tissues, septa; *ga*, ganglion cells of Auerbach's plexus; *ml*, longitudinal muscular coat; *p*, peritoneum (Schofield).

The function of Peyer's glands is by no means completely established: it was formerly believed that they discharged their contents into the intestine at intervals by rupture of their wall; but more recent acquaintance with the real structure of these bodies seems, however, to prove that they are rather to be regarded as structures analogous to lymphatic or absorbent glands, and that their office is to take up certain materials from the chyle, elaborate and subsequently discharge them into the lacteals, with which vessels they appear to be closely connected, although no direct communication has been proved to exist between them.

Fig. 155.*



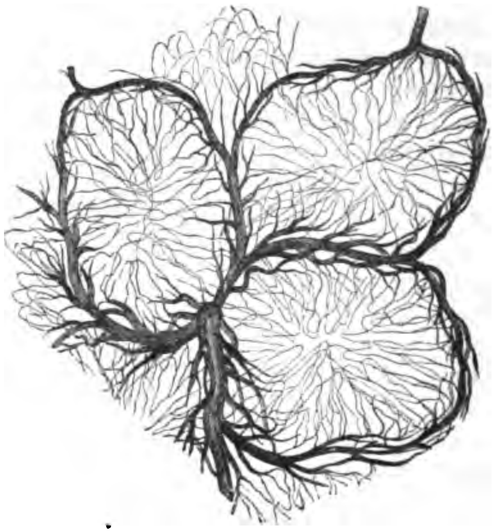
Moreover, it has been suggested that since the molecular and cellular contents of the glands are so abundantly traversed by minute blood-vessels, important changes may mutually take place between these contents and the blood in the vessels, material being extracted from the latter, elaborated by the cells, and then restored to the blood, much in the same manner as is believed to be the case in the so-called vascular glands, such as the spleen, thymus, and others; and that thus Peyer's glands should also be regarded as closely analogous to these vascular glands. Possibly they may combine the functions both of lymphatic and vascular glands, absorbing and elaborating material both from the chyle and from the blood within their minute vessels, and transmitting part to the lacteal system and part direct to the blood.

* Fig. 155. Side-view of a portion of intestinal mucous membrane of a cat, showing a Peyer's gland (*a*); it is imbedded in the submucous tissue (*f*), the line of separation between which and the mucous membrane passes across the gland: *b*, one of the tubular follicles, the orifices of which form the zone of openings around the gland: *c*, the fossa in the mucous membrane: *d*, villi; *e*, follicles of Lieberkühn: *m*, muscularis mucosæ (Bendz).

It is to be noted that they are largest and most prominent in children and young persons; during adult life they shrivel up and almost completely disappear.

Brunn's glands (fig. 157) are confined to the duodenum; they are most abundant and thickly set at the commencement of this portion of the intestine, diminishing gradually as the duodenum advances. Situated beneath the mucous membrane, and imbedded

Fig. 156.*

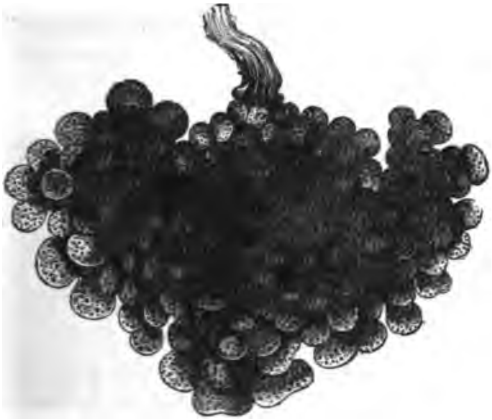


in the submucous tissue, they are minutely lobulated bodies visible to the naked eye, like detached small portions of pancreas, and provided with gland-ducts, which pass through the mucous membrane and open on the internal surface of the intestine. As in structure, so probably in function, they resemble the pancreas; or at least stand to it in a similar relation to that which the small labial and buccal glands occupy

* Fig. 156. Transverse section of injected Peyer's glands (from Kölliker). The drawing was taken from a preparation made by Frey: it represents the fine capillary looped network spreading from the surrounding blood-vessels into the interior of three of Peyer's capsules from the intestine of the rabbit.

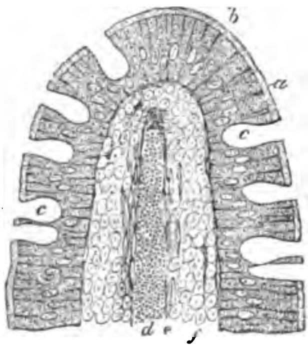
in relation to the larger salivary glands, the parotid and submaxillary.

Fig. 157.*



The *Villi* (figs. 154, 155, 158, and 159,) are confined exclusively to the mucous membrane of the *small* intestine. They are minute vascular processes, from a quarter of a line to a line and two-thirds in length, covering the surface of the mucous membrane, and giving it a peculiar velvety, fleecy appearance. Krause estimates them at fifty to ninety in number in a square line, at the upper part of the small intestine, and at forty to seventy in the same area at the lower part. They vary in form even in the same animal, and

Fig. 158.†



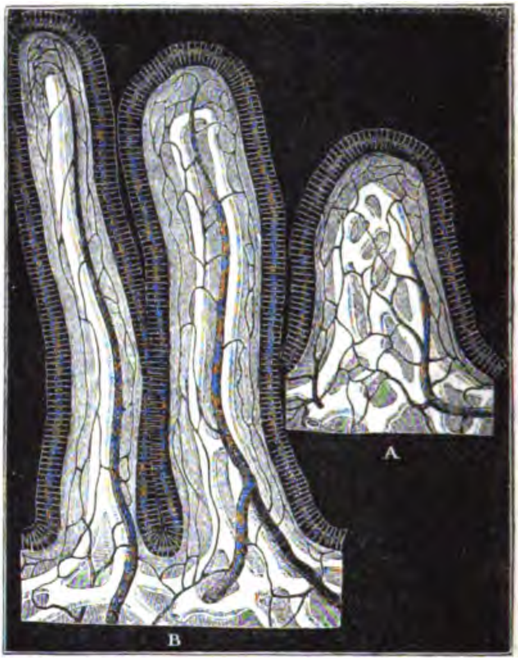
* Fig. 157. Enlarged view of one of Brunn's glands from the human duodenum. The main duct is seen superiorly; its branches are elsewhere hidden by the bunches of opaque glandular vesicles (Frey).

† Fig. 158. Vertical section of a villus of the small intestine of a cat. *a.* Striated basal border of the epithelium. *b.* Columnar epithelium. *c.* Goblet cells. *d.* Central lymph-vessel. *e.* Smooth muscular fibres. *f.* Adenoid stroma of the villus in which lymph corpuscles lie (Klein).

differ according as the lymphatic vessels they contain are empty or full of chyle; being usually, in the former case, flat and pointed at their summits, in the latter cylindrical or clavate.

Each villus consists of a small projection of mucous membrane, and its interior is therefore supported throughout by fine retiform

Fig. 159.*



or adenoid tissue, which forms the framework or stroma in which the other constituents are contained.

The surface of the villus is clothed by columnar epithelium, which rests on a fine basement membrane; while within this are found, reckoning from without inwards, blood-vessels, fibres of the *muscularis mucosæ*, and a single lymphatic or lacteal vessel

* Fig. 159. (Slightly altered from Teichmann.) A, Villus of sheep; B, Villi of man.

rarely looped or branched (fig. 159); besides granular matter, fat-globules, etc.

Fig. 160.*

The *epithelium* is of the columnar kind, and continuous with that lining the other parts of the mucous membrane. The cells are arranged with their long axis radiating from the surface of

* Fig. 160. A, lacteals in villi; P, Peyer's glands; B and D, superficial and deep network of lacteals in submucous tissue; L, Lieberkühn's glands; E, small branch of lacteal vessel on its way to mesenteric gland; H and O, muscular fibres of intestine; S, peritoneum (Teichmann).

the villus (fig. 158), and their smaller ends resting on the basement membrane. The free surface of the epithelial cells of the villi, like that of the cells which cover the general surface of the mucous membrane, is covered by a fine border which exhibits very delicate striations whence it derives its name, "striated basilar border." These striæ have given rise to the idea that it is traversed by a number of very fine canaliculi.

Beneath the basement or limiting membrane there is a rich supply of *blood-vessels.* Two or more minute arteries are distributed within each villus; and from their capillaries, which form a dense network, proceed one or two small veins, which pass out at the base of the villus.

The layer of the *muscularis mucosæ* in the villus forms a kind of thin hollow cone immediately around the central lacteal, and is, therefore, situate beneath the blood-vessels. The addition of acetic acid to the villus brings out the characteristic nuclei of the muscular fibres, and shows the size and position of the layer most distinctly. Its use is still unknown, although it is impossible to resist the belief, that it is instrumental in the propulsion of chyle along the lacteal.

The *lacteal vessel* enters the base of each villus, and passing up in the middle of it, extends nearly to the tip, where it ends commonly by a closed and somewhat dilated extremity. In the larger villi there may be two small lacteal vessels which end by a loop (fig. 159), or the lacteals may form a kind of network in the villus. The last method of ending, however, is rarely or never seen in the human subject, although common in some of the lower animals (A, fig. 159).

The office of the villi is the absorption of chyle from the completely digested food in the intestine. The mode in which they effect this will be considered in the Chapter on ABSORPTION.

Structure of the Large Intestine.

The Large Intestine, which in an adult is from about 4 to 6 feet long, is subdivided for descriptive purposes into three portions (fig. 134) viz.:—The *cæcum,* a short wide pouch, com-

municating with the lower end of the small intestine through an opening, guarded by the *ileo-cæcal* valve; the *colon*, continuous with the cæcum, which forms the principal part of the large intestine, and is divided into an ascending, transverse, and descending portion; and the *rectum*, which, after dilating at its lower part, again contracts, and immediately afterwards opens externally through the *anus*. Attached to the cæcum is the small *appendix vermiformis*.

Like the *small* intestine, the *large* is constructed of four principal coats, viz., the serous, muscular, submucous and mucous. The *serous* coat need not be here particularly described. Connected with it are the small processes of peritoneum containing fat, called *appendices epiploicæ*. The fibres of the *muscular* coat, like those of the small intestine, are arranged in two layers—the outer longitudinal, the inner circular. In the cæcum and colon, the longitudinal fibres, besides being, as in the small intestine, thinly disposed in all parts of the wall of the bowel, are collected, for the most part, into three strong bands, which being shorter, from end to end, than the other coats of the intestine, hold the canal in folds, bounding intermediate sacculi. On the division of these bands, the intestine can be drawn out to its full length, and it then assumes, of course, an uniformly cylindrical form. In the rectum, the fasiculi of these longitudinal bands spread out and mingle with the other longitudinal fibres, forming with them a thicker layer of fibres than exists on any other part of the intestinal canal. The circular muscular fibres are spread over the whole surface of the bowel, but are somewhat more marked in the intervals between the sacculi. Towards the lower end of the rectum they become more numerous, and at the anus they form a strong band called the *internal sphincter* muscle.

The *mucous membrane* of the large, like that of the small intestine, is lined throughout by columnar epithelium, but, unlike it, is quite smooth and destitute of villi, and is not projected in the form of *valvulæ conniventes*. Its general microscopic structure resembles that of the small intestine: and it is bounded below by the *muscularis mucosæ*.

The general arrangement of ganglia and nerve-fibres in the large intestine resembles that in the small (pp. 322–3).

Glands of the Large Intestine.—The glands with which the large intestine is provided are of two kinds, the *tubular* and *lenticular*.

The *tubular* glands, or glands of Lieberkühn, resemble those of the small intestine, but are somewhat larger and more numerous. They are also more uniformly distributed.

The *lenticular* glands are most numerous in the cæcum and vermiform appendix. They resemble in shape and structure, almost exactly, the solitary glands of the small intestine, and, like them, have no opening. Just over them, however, there is commonly a small depression in the mucous membrane, which has led to the erroneous belief that some of them open on the surface.

Ileo-cæcal valve.—The ileo-cæcal valve is situate at the place of junction of the small with the large intestine, and guards against any reflux of the contents of the latter into the ileum. It is composed of two semilunar folds of mucous membrane. Each fold is formed by a doubling inwards of the mucous membrane, and is strengthened on the outside by some of the circular muscular fibres of the intestine, which are contained between the outer surfaces of the two layers of which each fold is composed. The inner surface of the folds is smooth; the mucous membrane of the ileum being continuous with that of the cæcum. That surface of each fold which looks towards the small intestine is covered with villi, while that which looks to the cæcum has none. When the cæcum is distended, the margins of the folds are stretched, and thus are brought into firm apposition one with the other.

While the circular muscular fibres of the bowel at the junction of the ileum with the cæcum are contained between the outer opposed surfaces of the folds of mucous membrane which form the valve, the longitudinal muscular fibres and the peritoneum of the small and large intestine respectively are continuous with each other, without dipping in to follow the circular fibres and the mucous membrane. In this manner, therefore, the folding inwards of these two last named structures is preserved, while on the other hand, by dividing the longitudinal

muscular fibres and the peritoneum, the valve can be made to disappear, just as the constrictions between the sacculi of the large intestine can be made to disappear by performing a similar operation.

On account of the difficulty in isolating the secretion of the glands in the wall of the intestine (Brunn's and Lieberkühn's) from other secretions poured into the canal, (gastric juice, bile and pancreatic secretion), but little is known regarding the composition of the former fluid (intestinal juice, *succus entericus*).

It is said to be a yellowish alkaline fluid with a specific gravity of 1·011, and to contain about 2·5 per cent. of solid matters (Thiry).

Its functions probably resemble more or less nearly those of the pancreatic juice.

The length and complexity of the digestive tract seem to be closely connected with the character of the food on which an animal lives.

Thus, in all carnivorous animals such as the cat and dog, and pre-eminently in carnivorous birds, as hawks and herons, it is exceedingly short.

The seals, which, though carnivorous, possess a very long intestine, appear to furnish an exception ; but this is doubtless to be explained as an adaptation to their aquatic habits : their constant exposure to cold requiring that they should absorb as much as possible from their intestines.

Herbivorous animals, on the other hand, and the ruminants especially, have very long intestines (in the sheep 30 times the length of the body) which is no doubt to be connected with their lowly nutritious diet. In others, such as the rabbit, though the intestines are not excessively long, this is compensated by the great length and capacity of the cæcum. In man, the length of the intestines is intermediate between the extremes of the carnivora and herbivora, and his diet also is intermediate.

The Pancreas, and its Secretion.

The Pancreas is situated within the curve formed by the duodenum ; and its main duct opens into that part of the intestine, either through a small opening or through a duct common to itself and to the liver. The pancreas, in its minute anatomy, closely resembles the salivary glands ; and the fluid elaborated by it appears almost identical with saliva. The secretion of the pancreas has been obtained, for purposes of experiment, from

the lower animals, especially the dog, by opening the abdomen, and exposing the duct of the gland in such a manner as to establish a pancreatic fistula. An artificial pancreatic fluid may be obtained by acting either with water or glycerine on the pancreas of an animal, killed during the height of digestion.

When obtained pure, in all the different animals in which it has been hitherto examined, the secretion of the pancreas has been found colourless, transparent, and slightly viscid. It is alkaline when fresh, and contains a nitrogenous ferment named *pancreatin* and certain salts, both of which are very similar to those found in saliva. In pancreatic secretion, however, there is no sulpho-cyanogen. Like saliva, the pancreatic fluid, shortly after its escape, becomes neutral and then acid.

The following is the mean of three analyses of the pancreatic secretion of the dog by Schmidt :—

Composition of Pancreatic Secretion.

Water	980·45
Solids	19·55
Pancreatin	12·71
Inorganic bases and salts	6·84
	19·55

It has been estimated that 12 to 16 oz. av. of pancreatic fluid are secreted daily in the human subject.

The functions of the pancreas are as follows :—

1. Numerous experiments have shown, that *starch* is acted upon by the pancreatic secretion, or by portions of pancreas put in starch-paste, in the same manner that it is by saliva and portions of the salivary glands. And although, as before stated (p. 291), many substances besides those glands can excite the transformation of starch into dextrin and grape-sugar, yet it appears probable that the pancreatic fluid, exercising this power of transformation, is largely subservient to the purpose of digesting starch.

2. The existence of a pancreas in carnivora, which have little or no starch in their food, and the results of various observations

and experiments, leave very little doubt that the pancreatic secretion also assists largely in the digestion of *fatty matters*, partly by (*a*) causing them to split up into fatty acids and glycerin, the former combining with the alkalies present to from soaps, and partly (*b*) by transforming them into an emulsion, and thus rendering them capable of absorption by the lacteals. Several cases have been recorded in which the pancreatic duct being obstructed, so that the secretion could not be discharged, fatty or oily matter was abundantly discharged from the intestines. In nearly all these cases, indeed, the liver was coincidently diseased, and the change or absence of the bile might appear to contribute to the result; yet the frequency of extensive disease of the liver, unaccompanied by fatty discharges from the intestines, favours the view that, in these cases, it is to the absence of the pancreatic fluid from the intestines that the excretion or non-absorption of fatty matter should be ascribed. In Bernard's experiments too, fat always appeared in the evacuations when the pancreas was destroyed or its duct tied. Bernard, indeed, is of opinion that to emulsify fat is the express office of the pancreas, and the evidence that he and others have brought forward in support of this view is very weighty. The power of emulsifying fat, however, although perhaps mainly exercised by the secretion of the pancreas, is evidently possessed to some extent by other secretions poured into the intestines, and especially by the bile.

3. The pancreatic secretion discharges a third function also, namely, that of dissolving albuminous and gelatinous substances; the peptones produced by the action of the pancreatic secretion on proteids not differing essentially from those formed by the action of the gastric juice (p. 307).

By experiments with artificial pancreatic juice it is shown that before dissolving boiled fibrin, the pancreatic juice converts it into a soluble albuminous substance, very much like raw fibrin. "This is then dissolved, and is present in solution, either as albumen, coagulable by heat, or as an albuminate. The dissolved albumen is next converted into peptones. If the digestion is allowed to go on, the quantity of peptones in the solution diminishes, while that of leucin and tyrosin increases.

"Bodies which give the reaction of naphthilamine and indol (Kühne) are

also formed, and when the digestion goes on for a long time the indol is formed in considerable quantities, and emits a most disagreeable fæcal odour, which was attributed to putrefaction till Kühne showed its true nature" (Brunton).

Structure of the Liver.

The Liver is an extremely vascular organ, and receives its supply of blood from two distinct vessels, the *portal vein* and *hepatic artery*, while the blood is returned from it into the vena cava inferior by the *hepatic veins*. Its secretion, the *bile*, is con-

Fig. 161.*

veyed from it by the *hepatic duct*, either directly into the intestine, or, when digestion is not going on, into the *cystic* duct, and thence into the gall-bladder, where it accumulates until required.

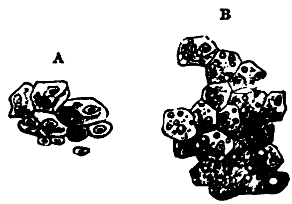
* Fig. 161. The liver has been turned over from left to right so as to expose the lower surface. 1, left lobe; 2, 3, 4, 5, right lobe; 6, lobulus quadratus; 7, pons hepatis; 8, 9, 10, lobulus Spigelii; 11, lobulus caudatus; 12, 13. transverse or portal fissure with the great vessels; 14, hepatic artery; 15, vena portæ; 16, anterior part of the longitudinal fissure, containing 17, the round ligament or obliterated remains of the umbilical vein; 18, posterior part of the same fissure, containing 19, the obliterated ductus venosus; 20, 21, 22, gall-bladder; 23, cystic duct; 24, hepatic duct; 25, fossa containing 26, the vena cava inferior; 27, opening of the capsular vein; 28, small part of the trunk of the right hepatic vein; 29, trunk of the left hepatic vein; 30, 31, openings of the right and left diaphragmatic veins.

The portal vein, hepatic artery, and hepatic duct branch together throughout the liver, while the hepatic veins and their tributaries run by themselves.

On the outside the liver has an incomplete covering of peritoneum, and beneath this is a very fine coat of areolar tissue, continuous over the whole surface of the organ. It is thickest where the peritoneum is absent, and is continuous on the general surface of the liver with the fine, and, in the human subject, almost imperceptible, areolar tissue investing the lobules. At the transverse fissure it is merged in the areolar investment called Glisson's capsule, which, surrounding the portal vein, hepatic artery, and hepatic duct, as they enter at this part, accompanies them in their branchings through the substance of the liver.

The liver is made up of small roundish or oval portions called *lobules*, each of which is about $\frac{1}{20}$ of an inch in diameter, and composed of the minute branches of the portal vein, hepatic artery, hepatic duct, and hepatic vein; while the interstices of these vessels are filled by the liver cells. The hepatic cells (fig. 162), which form the glandular or secreting part of the liver, are of a spheroidal form, somewhat polygonal from mutual pressure about $\frac{1}{800}$ to $\frac{1}{1000}$ inch in diameter, possessing one, sometimes two nuclei. The cell-substance contains numerous fatty molecules, and some yellowish-brown granules of bile-pigment. The cells sometimes exhibit slow amœboid movements. They are held together by a very delicate sustentacular tissue, continuous with the interlobular connective tissue.

*Fig. 162.**



To understand the distribution of the blood-vessels in the liver, it will be well to trace, first, the two blood-vessels and the duct which enter the organ on the under surface at the transverse

* Fig. 162. A, Liver-cells; B, ditto, containing various sized particles of fat.

fissure, viz., the portal vein, hepatic artery, and hepatic duct. As before remarked, all three run in company, and their appearance on longitudinal section is shown in fig. 163. Running together through the substance of the liver, they are contained in small channels called *portal canals*, their immediate investment being a sheath of areolar tissue (Glisson's capsule).

Fig. 163.*

To take the distribution of the portal vein first:—In its course through the liver this vessel gives off small branches, which divide and subdivide between the lobules surrounding them and limiting them, and from this circumstance called *inter*-lobular veins. From these small vessels a dense capillary network is prolonged into the substance of the lobule, and this network gradually gathering itself up, so to speak, into larger

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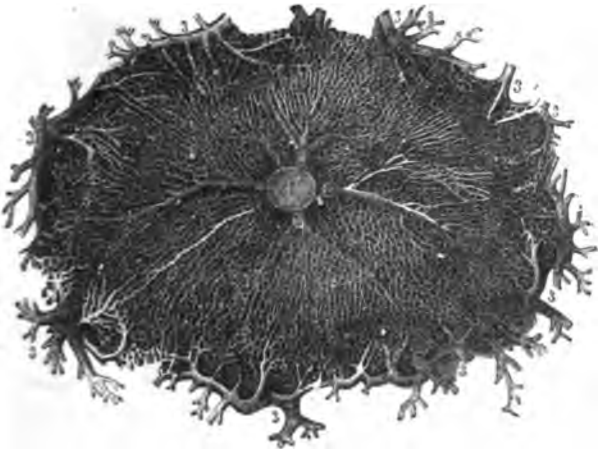
* Fig. 163. Longitudinal section of a portal canal, containing a portal vein, hepatic artery and hepatic duct, from the pig. P, branch of vena portæ. situate in a portal canal formed amongst the lobules of the liver, *l l*, and giving off vaginal branches; there are also seen within the large portal vein numerous orifices of the smallest interlobular veins arising directly from it; *a*, hepatic artery; *d*, hepatic duct. $\frac{5}{1}$. (Kiernan.)

vessels, converges finally to a single small vein, occupying the centre of the lobule, and hence called *intra*-lobular. This arrangement is well seen in fig. 164, which represents a transverse section of a lobule.

Fig. 164.*



The small *intra*-lobular veins discharge their contents into veins called *sub*-lobular (fig. 165); while these again, by their union, form the main branches of the *hepatic* veins, which leave the posterior border of the liver to end by two or three principal trunks in the inferior vena cava, just before its passage through the diaphragm. The *sub*-lobular and *hepatic veins*, unlike the *portal* vein and its companions, have little or no areolar tissue around them, and their coats being very thin, they form little more than mere channels in the liver substance which closely surrounds them.

The manner in which the lobules are connected with the

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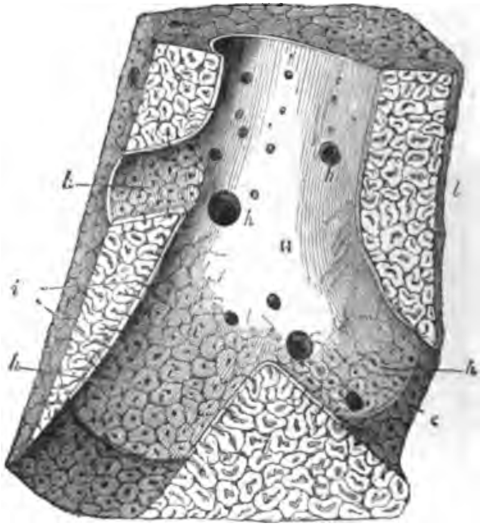
* Fig. 164. Cross section of a lobule of the human liver, in which the capillary network between the portal and hepatic veins has been fully injected. 1, Section of the *intra*-lobular vein; 2, its smaller branches collecting blood from the capillary network; 3, *inter*-lobular branches of the vena portæ with their smaller ramifications passing inwards towards the capillary network in the substance of the lobule. × 60. (Sappey.)

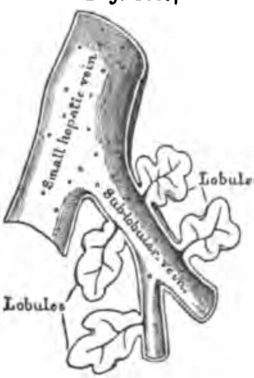
sublobular veins by means of the small *intralobular* veins is well seen in the diagram, fig. 165 and in fig. 166, which represent the

Fig. 165.*



parts as seen in a longitudinal section. The appearance has been likened to a twig having leaves without footstalks—the lobules representing the leaves, and the *sublobular* vein the small branch from which it springs. On a transverse section, the

Fig. 166.†

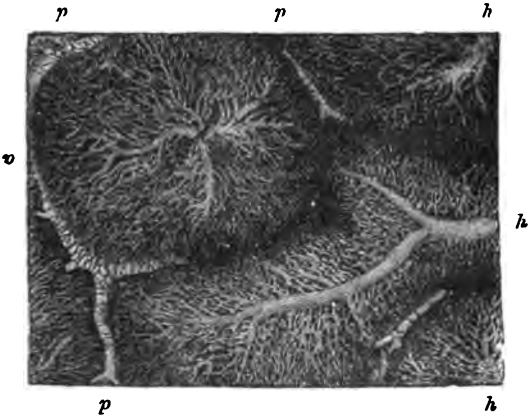


* Fig. 165. Section of a portion of liver passing longitudinally through a considerable hepatic vein, from the pig. H, hepatic venous trunk, against which the sides of the lobules (*l*) are applied; *h*, *h*, *h*, sublobular hepatic veins, on which the bases of the lobules rest, and through the coats of which they are seen as polygonal figures; *i*, mouth of the intralobular veins, opening into the sublobular veins; *i'*, intralobular veins shown passing up the centre of some divided lobules; *l*, *l*, cut surface of the liver; *c*, *c*, walls of the hepatic venous canal, formed by the polygonal bases of the lobules. × 5. (Kiernan.)

† Fig. 166. Diagram showing the manner in which the lobules of the liver rest on the sublobular veins (after Kiernan).

appearance of the *intralobular* veins is that of 1, fig. 164, while both a transverse and longitudinal section are exhibited in fig. 167.

Fig. 167.*



The hepatic artery, the function of which is to distribute blood for nutrition to Glisson's capsule, the walls of the ducts and blood-vessels, and other parts of the liver, is distributed in a very similar manner to the portal vein, its blood being returned by small branches either into the ramifications of the portal vein, or into the capillary plexus of the lobules which connects the *inter*- and *intra*-lobular veins.

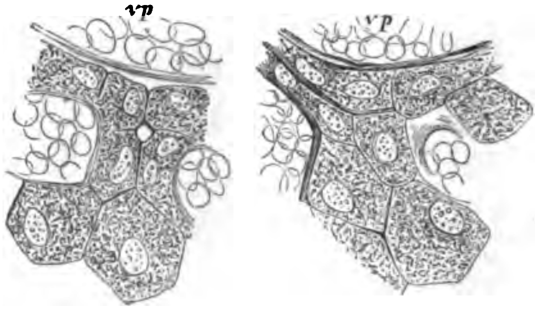
The hepatic duct divides and subdivides in a manner very like that of the portal vein and hepatic artery, the larger branches being lined by *cylindrical,* and the smaller by small *polygonal* epithelium. The exact arrangement of its terminal branches, however, and their relation to the liver-cells have not been agreed upon by different observers.

According to the most recent observations, the bile-capillaries

* Fig. 167. Capillary network of the lobules of the rabbit's liver (from Kölliker), $\frac{45}{1}$. The figure is taken from a very successful injection of the hepatic veins, made by Harting: it shows nearly the whole of two lobules, and parts of three others; *p*, portal branches running in the interlobular spaces; *h*, hepatic veins penetrating and radiating from the centre of the lobules.

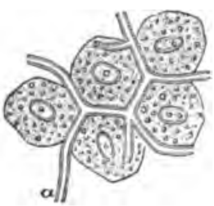
commence between the hepatic cells, and are bounded by a delicate membranous wall of their own.

Fig. 168.*



They appear to be always bounded by hepatic cells on either side, and are thus always separated from the nearest blood-capillary by at least the breadth of one cell (figs. 168 and 169).

Fig. 169.†



This view differs from that adopted by Beale in the fact that he believes that the wall of the terminal bile-ducts, instead of running in between the hepatic cells, invests a group of hepatic cells (fig. 170).

The Gall-bladder.

The Gall-bladder (21, fig. 161) is a pyriform bag, attached to the under surface of the liver, and supported also by the peri-

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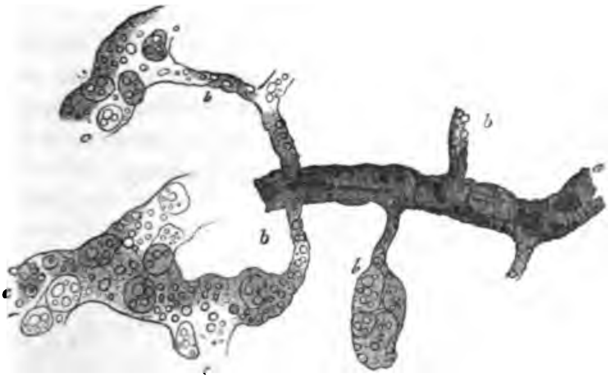
* Fig. 168. Hepatic cells and bile-capillaries, from the liver of a child three months old. Both figures represent fragments of a section carried through the periphery of a lobule. The red corpuscles of the blood are recognised by their circular contour : *v*, *p*, corresponds to an interlobular vein in immediate proximity with which are the epithelial cells of the biliary ducts to which, at the lower part of the figures, the much larger hepatic cells suddenly succeed (E. Hering).

† Fig. 169. A small fragment of an hepatic lobule, of which the smallest intercellular biliary ducts were filled with colouring matter during life, highly magnified (Chrzonszczewsky).

toneum, which passes below it. The larger end or *fundus*, projects beyond the front margin of the liver; while the smaller end contracts into the cystic duct (figs. 23, 161).

Fig. 170.*



Its walls are constructed of three principal coats. (1) Externally (excepting that part which is in contact with the liver), is the *serous* coat, which has the same structure as the peritoneum with which it is continuous. Within this is (2) the *fibrous* or areolar coat, constructed of tough fibrous and elastic tissue, with which is mingled a considerable number of plain muscular fibres, both longitudinal and circular. (3) Internally the gall-bladder is lined by mucous membrane, and a layer of columnar epithelium. The surface of the mucous membrane presents to the naked eye a minutely honey-combed appearance from a number of tiny polygonal depressions with intervening ridges, by which its surface is mapped out. In the cystic duct the mucous membrane is raised up in the form of crescentic folds, which together appear like a spiral valve, and which minister to the function of the gall-bladder in retaining the bile during the intervals of digestion.

* Fig. 170. View of some of the smallest biliary ducts illustrating Beale's view of their relation to the biliary cells (from Kölliker after Beale), $\frac{215}{1}$.

The drawing is taken from an injected preparation of the pig's liver; *a*, small branch of an interlobular hepatic duct; *b*, smallest biliary ducts; *c*, portions of the cellular part of the lobule in which the cells are seen within tubes which communicate with the finest ducts.

The gall-bladder and all the main biliary ducts are provided with mucous glands, which open on their internal surface.

Functions of the Liver.

The *Secretion of Bile* is the most obvious, and one of the chief functions which the liver has to perform; but, as will be presently shown, it is not the only one; for important changes are effected in certain constituents of the blood in its transit through this gland, whereby they are rendered more fit for their subsequent purposes in the animal economy.

The Bile.

Composition of the Bile.—The bile is a somewhat viscid fluid, of a yellow or greenish-yellow colour, a strongly bitter taste, and, when fresh, with a scarcely perceptible odour; it has a neutral or slightly alkaline reaction, and its specific gravity is about 1020. Its colour and degree of consistence vary much, apparently independent of disease; but, as a rule, it becomes gradually more deeply coloured and thicker as it advances along its ducts, or when it remains long in the gall-bladder, wherein, at the same time, it becomes more viscid and ropy, of a darker colour, and more bitter taste, mainly from its greater degree of concentration, on account of partial absorption of its water, but partly also from being mixed with mucus.

The following analysis is by Frerichs:—

Composition of Human Bile.

Water	859·2
Solids	140·8
	1,000·0

Biliary acids combined with alkalies	Bilin	91·5
Fat		9·2
Cholesterin		2·6
Mucus and colouring matters		29·8
Salts		7·7
		140·8

Bilin when freed by ether from the fat with which it is combined, is a resinoid substance, soluble in water, alcohol, and alkaline solutions, and giving to the watery solution the taste and general character of bile. It is a compound of soda, with two resinous acids, named glycocholic and taurocholic acids. The former consists of cholic acid conjugated with glycin (or sugar of gelatin), the latter of the same acid conjugated with taurin.

Fatty substances are found in variable proportions in the bile. Besides the ordinary saponifiable fats, there is a small quantity of cholesterin (p. 34), which, with the other free fats, is probably held in solution by the taurocholate of soda.

A peculiar substance, which Dr. Flint has discovered in the fæces, and named *stercorin* is closely allied to cholesterin; and Dr. Flint believes that while one great function of the liver is to excrete cholesterin from the blood, as the kidney excretes urea, the stercorin of fæces is the modified form in which cholesterin finally leaves the body. Ten grains and a half of stercorin, he reckons, are excreted daily.

Fig. 171.*

The yellow *colouring matter* of the bile of man and the Carnivora is termed *bilirubin* or *bilifulvin*; a green colouring matter, *biliverdin*, which always exists in large amount in the bile of Herbivora, being formed from bilirubin on exposure to the air, or by subjecting the bile to any other oxidising agency, as by adding nitric acid. When the bile has been long in the gall-bladder, a third pigment, *biliprasin*, may be also found in small amount. In cases of biliary obstruction, the colouring matter of the bile is re-absorbed, and circulates with the blood, giving to the tissues the yellow tint characteristic of jaundice.

There seems to be some relationship between the colour-matters of the blood and bile, and, it may be added, between

* Fig. 171. Crystalline scales of cholesterin.

these and that of the urine also; and it is probable they are, all of them, varieties of the same pigment, or derived from the same source. Nothing, however, is at present certainly known regarding the relation in which one of them stands to the other.

The *mucus* in bile is derived from the mucous membrane and glands of the gall-bladder, and of the hepatic ducts. It constitutes the residue after bile is treated with alcohol. The epithelium with which it is mixed may be detected in the bile with the microscope in the form of cylindrical cells, either scattered or still held together in layers. To the presence of the mucus is probably to be ascribed the rapid decomposition undergone by the bilin; for, according to Berzelius, if the mucus be separated, bile will remain unchanged for many days.

The *saline* or *inorganic constituents* of the bile are similar to those found in most other secreted fluids. It is possible that the carbonate and neutral phosphate of sodium and potassium, found in the ashes of bile, are formed in the incineration, and do not exist as such in the fluid. Oxide of iron is said to be a common constituent of the ashes of bile, and copper is generally found in healthy bile, and constantly in biliary calculi.

Such are the principal chemical constituents of bile; but its physiology is, perhaps, better illustrated by its ultimate elementary composition. According to Liebig's analysis, the biliary matter,—consisting of bilin and the products of its spontaneous decomposition—yields, on analysis, 76 atoms of carbon, 66 of hydrogen, 22 of oxygen, 2 of nitrogen, and a certain quantity of sulphur.* Comparing this with the ultimate composition of the organic parts of blood which may be stated at $C_{48}H_{36}N_6O_{14}$ with sulphur and phosphorus—it is evident that bile contains a large preponderance of carbon and hydrogen, and a deficiency of nitrogen. The import of this will presently appear.

TESTS FOR BILE.—A common test for the presence of bile consists of the addition of a small quantity of nitric acid, when, if bile be present, a play of colours is produced, beginning with green and passing through various tints to red. This test will detect only the *colouring matter* of the bile.

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* The sulphur is combined with the taurin—one of the substances yielded by the decomposition of bilin. According to Dr. Kemp, the sulphur in the bile of the ox, dried and freed from mucus, colouring matter, and salts, constitutes about 3 per cent.

The best test for the *bilin* is Pettenkofer's. To the liquid suspected to contain bile must be added, first, a drop or two of a strong solution of cane-sugar (one part of sugar to four parts of water), and immediately afterwards sulphuric acid, to the extent of about two-thirds of the liquid. On first adding the acid, a whitish precipitate falls; but this redissolves with a slight excess of the acid, and on the further addition of the latter there appears a bright cherry-red colour, gradually changing through a lake tint, to a dark purple.

The *process of secreting bile* is continually going on, but appears to be retarded during fasting, and accelerated on taking food. This was shown by Blondlot who, having tied the common bile-duct of a dog, and established a fistulous opening between the skin and gall-bladder, whereby all the bile secreted was discharged at the surface, noticed that when the animal was fasting, sometimes not a drop of bile was discharged for several hours; but that, in about ten minutes after the introduction of food into the stomach, the bile began to flow abundantly, and continued to do so during the whole period of digestion. Bidder and Schmidt's observations are quite in accordance with this.

The bile is formed in the hepatic cells; then, being discharged into the minute hepatic ducts, it passes into the larger trunks, and from the main hepatic duct may be carried at once into the duodenum. But, probably, this happens only while digestion is going on; during fasting, it regurgitates from the common bile-duct through the cystic duct, into the gall-bladder, where it accumulates till, in the next period of digestion, it is discharged into the intestine. The gall-bladder thus fulfils what appears to be its chief or only office, that of a reservoir; for its presence enables bile to be constantly secreted, yet insures that it shall all be employed in the service of digestion, although digestion is periodic, and the secretion of bile constant.

The mechanism by which the bile passes into the gall-bladder is simple. The orifice through which the common bile-duct communicates with the duodenum is narrower than the duct, and appears to be closed, except when there is sufficient pressure

behind to force the bile through it. The pressure exercised upon the bile secreted during the intervals of digestion appears insufficient to overcome the force with which the orifice of the duct is closed; and the bile in the common duct, finding no exit in the intestine, traverses the cystic duct, and so passes into the gall-bladder, being probably aided in this retrograde course by the peristaltic action of the ducts. The bile is discharged from the gall-bladder and enters the duodenum on the introduction of food into the small intestine: being pressed on by the contraction of the coats of the gall-bladder, and of the common bile-duct also; for both these organs contain unstriped muscular fibre-cells. Their contraction is excited by the stimulus of the food in the duodenum acting so as to produce a reflex movement, the force of which is sufficient to open the orifice of the common bile-duct.

Various estimates have been made of the *quantity* of bile discharged into the intestines in twenty-four hours: the quantity doubtless varying, like that of the gastric fluid, in proportion to the amount of food taken. A fair average of several computations would give thirty to forty ounces as the quantity daily secreted by man.

Bile, as such, is not preformed in the blood. As just observed, it is formed by the hepatic cells. When it is, however, prevented by an obstruction of some kind, from escaping into the intestine (as by the passage of a *gall-stone* along the hepatic duct) it is absorbed in great excess, into the blood, and, circulating with it, gives rise to the well-known phenomena of jaundice.

The *purposes served by the secretion of bile* may be considered to be of two principal kinds, viz., *excrementitious* and *digestive*.

As an excrementitious substance, the bile may serve especially as a medium for the separation of excess of carbon and hydrogen from the blood; and its adaptation to this purpose is well illustrated by the peculiarities attending its secretion and disposal in the fœtus. During intra-uterine life, the lungs and the intestinal canal are almost inactive; there is no respiration of open air or digestion of food; these are unnecessary, on account of the supply of well elaborated nutriment received by the vessels of the fœtus at

the placenta. The liver, during the same time, is proportionally larger than it is after birth, and the secretion of bile is active, although there is no food in the intestinal canal upon which it can exercise any digestive property. At birth, the intestinal canal is full of thick bile, mixed with intestinal secretion; for the *meconium*, or fæces of the fœtus, are shown by the analyses of Simon and of Frerichs to contain all the essential principles of bile.

Composition of Meconium (Frerichs):

Biliary resin	15·6
Common fat and cholesterin	15·4
Epithelium, mucus, pigment, and salts	69·
	100·

In the fœtus, therefore, the main purpose of the secretion of bile must be the purification of the blood by *direct* excretion, *i.e.*, by separation from the blood, and ejection from the body without further change. Probably all the bile secreted in fœtal life is incorporated in the meconium, and with it discharged, and thus the liver may be said to discharge a function in some sense vicarious of that of the lungs. For, in the fœtus, nearly all the blood coming from the placenta passes through the liver, previous to its distribution to the several organs of the body; and the abstraction of carbon, hydrogen, and other elements of bile will purify it, as in extra-uterine life it is purified by the separation of carbonic acid and water at the lungs.

The evident disposal of the fœtal bile by excretion, makes it highly probable that the bile in extra-uterine life is also, at least in part, destined to be discharged as excrementitious. But the analysis of the fæces of both children and adult shows that (except when rapidly discharged in purgation) they contain very little of the bile secreted, probably not more than one-sixteenth part of its weight, and that this portion includes chiefly its colouring, and some of its fatty matters, and, to only a very slight degree, its essential principle, the *bilin*. Almost all the bilin is again absorbed from the intestines into the blood. But the elementary composition of bilin (see p. 350) shows such a preponderance of carbon and hydrogen, that probably, after

absorption, it combines with oxygen, and is excreted in the form of carbonic acid and water.

The change after birth, from the direct to the indirect mode of excretion of the bile may, with much probability, be connected with a purpose in relation to the development of heat. The temperature of the fœtus is maintained by that of the parent, and needs no source of heat within the body of the fœtus itself; but, in extra-uterine life, there is (as one may say) a waste of material for heat when any excretion is discharged unoxidized; the carbon and hydrogen of the bilin, therefore, instead of being ejected in the fæces, are re-absorbed, in order that they may be combined with oxygen, and that in the combination, heat may be generated.

According to Dr. Flint, the excretion of *cholesterin*, must be regarded as an important function of the liver; this substance being altered in its passage through the intestine and appearing in the fæces in the form of *stercorin* (p. 365).

From the peculiar manner in which the liver is supplied with much of the blood that flows through it, it is probable, as Dr. Budd suggests, that this organ is excretory, not only for such hydro-carbonaceous matters as may need expulsion from any portion of the blood, but that it serves for the direct purification of the stream which, arriving by the portal vein, has just gathered up various substances in its course through the digestive organs—substances which may need to be expelled, almost immediately after their absorption. For it is easily conceivable that many things may be taken up during digestion, which not only are unfit for purposes of nutrition, but which would be positively injurious if allowed to mingle with the general mass of the blood. The liver, therefore, may be supposed placed in the only road by which such matters can pass unchanged into the general current, jealously to guard against their further progress, and turn them back again into an excretory channel. The frequency with which metallic poisons are either excreted by the liver or intercepted and retained, often for a considerable time, in its own substance, may be adduced as evidence for the probable truth of this supposition.

Though one chief purpose of the secretion of bile may thus appear to be the purification of the blood by ultimate excretion, yet there are many reasons for believing that, while it is in the intestines, it performs an important part in the process of digestion. In nearly all animals, for example, the bile is discharged, not through an excretory duct communicating with the external surface or with a simple reservoir, as most excretions are, but is made to pass into the intestinal canal, so as to be mingled with the chyme directly after it leaves the stomach; an arrangement, the constancy of which clearly indicates that the bile has some important relations to the food with which it is thus mixed. A similar indication is furnished also by the fact that the secretion of bile is most active, and the quantity discharged into the intestines much greater, during digestion than at any other time; although, without doubt, this activity of secretion during digestion may, however, be in part ascribed to the fact that a greater quantity of blood is sent through the portal vein to the liver at this time, and that this blood contains some of the materials of the food absorbed from the stomach and intestines, which may need to be excreted, either temporarily, (to be afterwards reabsorbed,) or permanently.

Respecting the functions discharged by the bile in digestion, there is little doubt that it (1.) assists in emulsifying the fatty portions of the food, and thus rendering them capable of being absorbed by the lacteals. For it has appeared in some experiments in which the common bile-duct was tied, that although the process of digestion in the stomach was unaffected, chyle was no longer well-formed; the contents of the lacteals consisting of clear, colourless fluid, instead of being opaque and white, as they ordinarily are, after feeding.

(2.) It is probable, also, from the result of some experiments by Wistinghausen and Hoffmann, that the moistening of the mucous membrane of the intestines by bile facilitates absorption of fatty matters through it.

(3.) The bile, like the gastric fluid, has a considerable antiseptic power, and may serve to prevent the decomposition of food during the time of its sojourn in the intestines. The experiments of

Tiedemann and Gmelin show that the contents of the intestines are much more fœtid after the common bile-duct has been tied than at other times; and the experiments of Bidder and Schmidt on animals with an artificial biliary fistula, confirm this observation; moreover, it is found that the mixture of bile with a fermenting fluid stops or spoils the process of fermentation.

(4.) The bile has also been considered to act as a kind of natural purgative, by promoting an increased secretion of the intestinal glands, and by stimulating the intestines to the propulsion of their contents. This view receives support from the constipation which ordinarily exists in jaundice, from the diarrhœa which accompanies excessive secretion of bile, and from the purgative properties of ox-gall.

Nothing is known with certainty respecting the changes which the re-absorbed portions of the bile undergo. That they are much changed appears from the impossibility of detecting them in the blood; and that part of this change is effected in the liver is probable from an experiment of Magendie, who found that when he injected bile into the portal vein, a dog was unharmed, but was killed when he injected the bile into one of the systemic vessels.

The secretion of bile, as already observed, is only one of the purposes fulfilled by the liver. Another very important function appears to be that of so acting upon certain constitutents of the blood passing through it, as to render some of them capable of assimilation with the blood generally, and to prepare others for being duly eliminated in the process of respiration. From the labours of M. Bernard, to whom we owe most of what we know on this subject, it appears that the peptones (p. 308), conveyed from the alimentary canal by the blood of the portal vein, require to be submitted to the influence of the liver before they can be assimilated by the blood; for if such albuminous matter is injected into the jugular vein, it speedily appears in the urine; but if introduced into the portal vein, and thus allowed to traverse the liver, it is no longer ejected as a foreign substance, but is incorporated with the albuminous part of the blood.

Albuminous matters are also subject to decomposition by the liver in another way to be immediately noticed (p. 358).

It is a remarkable fact that bile causes the precipitation of the peptones in the duodenum.

Glycogenic Function of the Liver.

The important fact that the liver normally forms *glucose* or grape sugar, or a substance readily convertible into it, was discovered by Claude Bernard in 1848, in the course of some experiments which he undertook for the purpose of finding out in what part of the circulatory system the saccharine matter disappeared, which was absorbed from the alimentary canal.

With this purpose he fed a dog for seven days with food containing a large quantity of sugar and starch; and, as might be expected, found sugar in both the portal and hepatic veins. He then fed a dog with meat only, and, to his surprise, still found sugar in the hepatic veins. Repeated experiments gave invariably the same result; no sugar being found, under a meat diet, in the portal vein, if care were taken, by applying a ligature on it at the transverse fissure, to prevent reflux of blood from the hepatic venous system. Bernard found sugar also in the substance of the liver. It thus seemed certain that the liver formed sugar, even when from the absence of saccharine and amyloid matters in the food, none could be brought directly to it from the stomach or intestines.

Excepting cases in which large quantities of starch and sugar were taken as food, no sugar was found in the blood after it had passed through the lungs; the sugar formed by the liver, having presumably disappeared by combustion, in the course of the pulmonary circulation.

Bernard found, subsequently to the before-mentioned experiments, that a liver, removed from the body, and from which all sugar had been completely washed away by injecting a stream of water through its blood-vessels, will be found, after the lapse of a few hours, to contain sugar in abundance.

This *post-mortem* production of sugar was a fact which could only be explained in the supposition that the liver contained a

substance, readily convertible into sugar in the course merely of post-mortem decomposition; and this theory was proved correct by the discovery of a substance in the liver allied to starch, and now generally termed *glycogen.*

We may believe, therefore, that the liver does not form sugar directly from the materials brought to it by the blood, but that glycogen is first formed and stored in its substance; and that the sugar when present, is the result of the transformation of the latter.

Although, as before mentioned, glycogen is produced by the liver when neither starch nor sugar is present in the food, its amount is much less under such a diet. This is well shown by Pavy's experiments, which may be thus tabulated:—

Average amount of Glycogen in the Liver of Dogs under various Diets.

Diet.	Amount of Glycogen in Liver.
Animal food	7·19 per cent.
Animal food with sugar (about ¼ lb. of sugar daily)	14·5 „
Vegetable diet (potatoes, with bread or barley-meal)	17·23 „

The dependence of the formation of glycogen on the food taken is also well shown by the following results, obtained by the same experimenter:—

Average quantity of Glycogen found in the Liver of Rabbits after Fasting, and after a Diet of Starch and Sugar respectively.

	Average amount of Glycogen in Liver.
After fasting for three days	Practically absent.
„ diet of starch and grape-sugar . . .	15·4 per cent.
„ „ cane sugar	16·9 „

Regarding these facts there is no dispute. All are agreed that glycogen is formed, and laid up in store, temporarily, by the liver-cells; and that it is not formed exclusively from saccharine and amylaceous foods, but from albuminous substances also; the albumen, in the latter case, being probably split up into glycogen which is temporarily stored in the liver, and urea which is excreted by the kidneys.

There is not, however, agreement among physiologists as to the ultimate destination of glycogen.

There are two chief theories on the subject. (1.) According to Bernard and most other physiologists, the conversion of glycogen into sugar takes place rapidly during life by the agency of a

ferment also formed in the liver; and the sugar is conveyed away by the blood of the hepatic veins, and probably at once undergoes combustion. (2.) Pavy and others believe that the conversion into sugar only occurs after death, and that during life no sugar exists in healthy livers, glycogen not undergoing transformation. The chief arguments advanced by Pavy in support of this view are, (*a*) that scarcely a trace of sugar is found in blood drawn during life from the right ventricle, or in blood collected from the right side of the heart *immediately* after an animal has been killed; while if the examination be delayed for a very short time after death, sugar in abundance may be found in such blood; (*b*), that the liver, like the venous blood in the heart, is, at the moment of death, completely free from sugar, although afterwards its tissue speedily becomes saccharine, unless the formation of sugar be prevented by freezing, boiling, or other means calculated to interfere with the action of a ferment on the amyloid substance of the organ. Instead of adopting Bernard's view, that normally, during life, glycogen passes as sugar into the hepatic venous blood, and thereby is conveyed to the lungs to be further disposed of, Pavy inclines to the belief that it may represent an intermediate stage in the formation of fat from materials absorbed from the alimentary canal.

To demonstrate the presence of sugar in the liver, a portion of this organ, after being cut into small pieces, is bruised in a mortar to a pulp with a small quantity of water, and the pulp is boiled with sodium-sulphate in order to precipitate albuminous and colouring matters. The decoction is then filtered and may be tested for glucose. The most usual test is Trommer's. To the filtered solution an equal quantity of liquor potassæ is added, with a few drops of a solution of sulphate of copper. The mixture is then boiled, when the presence of sugar is indicated by a reddish-brown precipitate of the suboxide of copper.

Glycogen ($C_6H_{12}O_6$) is obtained by taking a portion of liver from a recently killed animal, and, after cutting it into small pieces, placing it for a short time in boiling water. It is then bruised in a mortar, until it forms a pulpy mass, and subsequently boiled in distilled water for about a quarter of an hour. The glycogen is precipitated from the filtered decoction by the addition of alcohol.

When purified, glycogen is a white, amorphous, starch-like substance, odourless and tasteless, soluble in water, insoluble in alcohol. It is converted into glucose by boiling with dilute acids, or by contact with any animal ferment.

Glycogen has been found in many other structures than the liver (p. 35).

The facility with which the glycogen of the liver is transformed into sugar would lead to the expectation that this chemical change, under many circumstances, would occur to such an extent that sugar would be present not only in the hepatic veins, but in the blood generally. Such is frequently the case; the sugar when in excess in the blood being secreted by the kidneys, and thus appearing in variable quantities in the urine (Glycosuria).

Certain injuries to the nervous system will cause glycosuria, *e.g.*, puncture of the floor of the fourth ventricle (Bernard); section of the cervical sympathetic (Pavy); section of the inferior cervical ganglion (Eckhard); irritation of the central extremity of the divided pneumogastric (Schiff, Moos). All these act by modifying the blood-circulation through the liver—probably by causing paralysis of the hepatic vaso-motor nerves.

Many other circumstances will cause glycosuria. It has been observed after the administration of various drugs, after the injection of *curare* (Schiff), poisoning with carbonic oxide gas (Schiff, Richardson), the inhalation of ether, chloroform, etc., (Harley), the injection of oxygenated blood into the portal venous system (Pavy). It has been observed in man after injuries to the head, and in the course of various diseases.

The well-known disease, *diabetes mellitus*, in which a large quantity of sugar is persistently secreted daily with the urine, has, doubtless, some close relation to the normal glycogenic function of the liver; but the nature of the relationship is at present quite unknown.

Summary of the Changes which take place in the Food during its Passage through the Small Intestine.

In order to understand the changes in the food which occur during its passage through the small intestine, it will be well to refer briefly to the state in which it leaves the stomach through the pylorus. It has been said before, that the chief office of the stomach is not only to mix into an uniform mass all the varieties

of food that reach it through the œsophagus, but especially to dissolve the nitrogenous portion by means of the gastric juice. The fatty matters, during their sojourn in the stomach, become more thoroughly mingled with the other constituents of the food taken, but are not yet in a state fit for absorption. The conversion of starch into sugar, which began in the mouth, has been interfered with, although not stopped altogether. The soluble matters—both those which were so from the first, as sugar and saline matter, and those which have been made so by the action of the saliva and gastric juice—have begun to disappear by absorption into the blood-vessels, and the same thing has befallen such fluids as may have been swallowed,—wine, water, etc.

The thin pultaceous chyme, therefore, which, during the whole period of gastric digestion, is being constantly squeezed or strained through the pyloric orifice into the duodenum, consists of albuminous matter, broken down, dissolving and half dissolved; fatty matter, broken down, but not dissolved at all; starch very slowly in process of conversion into sugar, and as it becomes sugar, also dissolving in the fluids with which it is mixed; while with these are mingled gastric fluid, and fluid that has been swallowed, together with such portions of the food as are not digestible, and will be finally expelled as part of the fæces.

On the entrance of the chyme into the duodenum, it is subjected to the influence of the fluid secreted by Lieberkühn's and Brunn's glands, before described, and to that of the bile and pancreatic juice, which are poured into this part of the intestine. All these secretions have a more or less alkaline reaction, and by their admixture with the gastric chyme, its acidity becomes less and less until at length, at about the middle of the small intestine, the reaction becomes alkaline and continues so far as the ileo-cæcal valve.

The special digestive functions of the small intestine may be best described under the following heads:—

(1.) Without doubt, that part of digestion which it is one important duty of the small intestine to perform, is the alteration of the *fat* in such a manner as to make it fit for absorption. And

there is no doubt that this change is chiefly effected in the upper part of the small intestine. What is the exact share of the process, however, allotted respectively to the bile, pancreatic secretion, and the secretion of the intestinal glands, is still uncertain,—probably the pancreatic juice is the most important. The fat is changed in two ways. (*a*). To a slight extent it is chemically decomposed by the alkaline secretions with which it is mingled, and a soap is the result. (*b*). It is emulsionised, *i.e.*, its particles are minutely subdivided and diffused, so that the mixture assumes the condition of a milky fluid, or emulsion.

During digestion in the small intestine, the villi become turgid with blood, their epithelial cells become filled, by absorption, with fat-globules, which, after minute division, transude into the lymphoid tissue of the villus, and thence into the lacteal vessel in the centre, whence they pass to the lymphatic plexus of the submucous tissue, and, ultimately, by way of the lymph-vessels of the mesentery, to the thoracic duct. A small part of the fat which is saponified, is also absorbed by the blood-vessels of the intestine.

The term chyle is sometimes applied to the emulsified contents of the intestine after their admixture with the bile and pancreatic juice; but, more strictly, to the fluid contained in the lacteal vessels during digestion, which differs from ordinary lymph contained in the same vessels at other times, chiefly in the greatly increased quantity of fat which has been absorbed from the small intestine.

(2). The *albuminous* substances which have been partly dissolved in the stomach, continue to be acted on by the gastric juice which passes into the duodenum with them, and the effect of the last-named secretion is assisted by that of the pancreas and intestinal glands. *Albuminous* substances, which are chemically altered in the process of digestion (peptones, p. 307), and gelatinous matters similarly changed, are absorbed by both the blood-vessels and lymphatics of the intestinal mucous membrane. Albuminous matters, in a state of solution, which have not undergone the peptonic change, are probably, from the difficulty with which they diffuse, absorbed, if at all, almost solely by the lymphatics.

(3). The *starchy*, or amyloid portions of the food, the conversion of which into dextrin and sugar was more or less interrupted during its stay in the stomach (p. 308), is now acted on briskly by the secretion of the pancreas, and of Brunn's glands, and perhaps of Lieberkühn's glands also; and the sugar, as it is formed, is dissolved in the intestinal fluids, and is absorbed chiefly by the blood-vessels.

(4). Saline and saccharine matters, as common salt, and cane sugar, if not in a state of solution beforehand in the saliva or other fluids which may have been swallowed with them, are at once dissolved in the stomach, and if not here absorbed, are soon taken up in the small intestine; the blood-vessels, as in the last case, being chiefly concerned in the absorption. Cane sugar is in part or wholly converted into grape-sugar before its absorption.

(5). The *liquids*, including in this term the ordinary drinks, as water, wine, ale, tea, etc., which may have escaped absorption in the stomach, are absorbed probably very soon after their entrance into the intestine; the fluidity of the contents of the latter being preserved more by the constant secretion of fluid by the intestinal glands, pancreas, and liver, than by any given portion of fluid, whether swallowed or secreted, remaining long unabsorbed. From this fact, therefore, it may be gathered that there is a kind of circulation constantly proceeding from the intestines into the blood, and from the blood into the intestines again; for as all the fluid—a very large amount—secreted by the intestinal glands, must come from the blood, the latter would be too much drained, were it not that the same fluid after secretion is again re-absorbed into the current of blood—going into the blood charged with nutrient products of digestion—coming out again by secretion through the glands in a comparatively uncharged condition.

At the lower end of the small intestine, the chyme, still thin and pultaceous, is of a light yellow colour, and has a distinctly fæcal odour. In this state it passes through the ileo-cæcal opening into the large intestine.

Summary of the Process of Digestion in the Large Intestine.

The changes which take place in the chyme after its passage from the *small* into the *large* intestine are probably only the continuation of the same changes that occur in the course of the food's passage through the upper part of the intestinal canal. From the absence of villi, however, we may conclude that absorption, especially of fatty matter, is in great part completed in the small intestine; while, from the still half-liquid, pultaceous consistence of the chyme when it first enters the cæcum, there can be no doubt that the absorption of liquid is not by any means concluded. The peculiar odour, moreover, which is acquired after a short time by the contents of the large bowel, would seem to indicate a further chemical change in the alimentary matters or in the digestive fluids, or both (pp. 339–340). The acid reaction, which had become less and less distinct in the small bowel, again becomes very manifest in the cæcum—probably from acid fermentation processes in some of the materials of the food.

There seems no reason, however, to conclude that any special 'secondary,' digestive process occurs in the cæcum or in any other part of the large intestine. Probably any constituent of the food which has escaped digestion and absorption in the small bowel may be digested in the large intestine; and the power of this part of the intestinal canal to digest fatty, albuminous, or other matters, may be gathered from the good effects of nutrient enemata, so frequently given when from any cause there is difficulty in introducing food into the stomach. In ordinary healthy digestion, however, the changes which ensue in the chyme after its passage into the large intestine, are mainly the absorption of the more liquid parts, and the completion of the changes which were proceeding in the small intestine,—the process being assisted by the secretion of the numerous tubular glands therein present.

By these means the contents of the large intestine, as they proceed towards the rectum, become more and more solid, and losing their more liquid and nutrient parts, gradually acquire

the odour and consistence characteristic of fæces. After a sojourn of uncertain duration in the sigmoid flexure of the colon, or in the rectum, they are finally expelled by the contraction of its muscular coat, aided, under ordinary circumstances, by the contraction of the abdominal muscles.

The average quantity of solid fæcal matter evacuated by the human adult in twenty-four hours is about six or eight ounces; an uncertain proportion of which consists simply of the undigested or chemically modified residue of the food; while the remainder consists of certain matters which are excreted into the intestinal canal.

Composition of Fæces.

Water		733·00
Solids		267·00
Special excrementitious constituents:—Excretin, excretoleic acid (Marcet), and stercorin (Austin Flint). Salts:—Chiefly phosphate of magnesium and phosphate of calcium, with small quantities of iron, soda, lime, and silica. Insoluble residue of the food (chiefly starch grains, woody tissue, particles of cartilage and fibrous tissue, undigested muscular fibres or fat, and the like, with insoluble substances accidentally introduced with the food. Mucus, epithelium, altered colouring matter of bile, fatty acids, etc. Varying quantities of other constituents of bile, and derivatives from them.	267·00	

The time occupied by the journey of a given portion of food from the stomach to the anus, varies considerably even in health, and on this account, probably, it is that such different opinions have been expressed in regard to the subject. Dr. Brinton supposes twelve hours to be occupied by the journey of an ordinary meal through the *small* intestine, and twenty-four to thirty-six hours by the passage through the *large* bowel.

Defæcation.

Immediately before the act of voluntary expulsion of fæces (*defæcation*) there is usually, first an inspiration, as in the case of coughing, sneezing, and vomiting; the glottis is then closed, and

the diaphragm fixed as in vomiting. Now, however, both the rima glottidis and the cardiac opening of the stomach remain closed, and the sphincter of the rectum, being relaxed, the evacuation of its contents takes place accordingly; the effect being, of course, increased by the muscular and elastic contraction of its own walls. As in the other actions just referred to, there is as much tendency to the escape of the contents of the lungs or stomach as of the rectum; but the pressure is relieved only at the orifice, the sphincter of which instinctively or involuntarily yields (see fig. 133).

On the Gases contained in the Stomach and Intestines.

It need scarcely be remarked that, under ordinary circumstances, the alimentary canal contains a considerable quantity of gaseous matter. Any one who has had occasion, in a post-mortem examination, either to lay open the intestines, or to let out the gas which they contain, must have been struck by the small space afterwards occupied by the bowels, and by the large degree, therefore, in which the gas, which naturally distends them, contributes to fill the cavity of the abdomen. Indeed, the presence of air in the intestines is so constant, and, within certain limits, the amount in health so uniform, that there can be no doubt that its existence here is not a mere accident, but intended to serve a definite and important purpose, although, probably, a mechanical one.

The sources of the gas contained in the stomach and bowels may be thus enumerated—

1. Air introduced in the act of swallowing either food or saliva.

2. Gases developed by the decomposition of alimentary matter or of the secretions and excretions mingled with it in the stomach and intestines.

3. It is probable that a certain mutual interchange occurs between the gases contained in the alimentary canal, and those present in the blood of the gastric and intestinal blood-vessels; but the conditions of the exchange are not known, and it is very doubtful whether anything like a true and definite secretion of

gas from the blood into the intestines or stomach ever takes place. There can be no doubt, however, that the intestines may be the proper excretory organs for many odorous and other substances, either absorbed from the air taken into the lungs in inspiration, or absorbed in the upper part of the alimentary canal, again to be excreted at a portion of the same tract lower down—in either case assuming rapidly a gaseous form after their excretion, and in this way, perhaps, obtaining a more ready egress from the body.

It is probable that, under ordinary circumstances, the gases of the stomach and intestines are derived chiefly from the second of the sources which have been enumerated.

Tabular Analysis of Gases contained in the Alimentary Canal.

<table>
<tr><th rowspan="2">Whence obtained.</th><th colspan="6">Composition by Volume.</th></tr>
<tr><th>Oxygen</th><th>Nitrog.</th><th>Carbon. Acid.</th><th>Hydrog</th><th>Carburet. Hydrogen.</th><th>Sulphuret. Hydrogen.</th></tr>
<tr><td>Stomach</td><td>11</td><td>71</td><td>14</td><td>4</td><td>—</td><td>—</td></tr>
<tr><td>Small Intestines</td><td>—</td><td>32</td><td>30</td><td>38</td><td>—</td><td rowspan="4">trace.</td></tr>
<tr><td>Cæcum</td><td>—</td><td>66</td><td>12</td><td>8</td><td>13</td></tr>
<tr><td>Colon</td><td>—</td><td>35</td><td>57</td><td>6</td><td>8</td></tr>
<tr><td>Rectum</td><td>—</td><td>46</td><td>43</td><td>—</td><td>11</td></tr>
<tr><td>Expelled *per anum*</td><td>—</td><td>22</td><td>41</td><td>19</td><td>19</td><td>½</td></tr>
</table>

The above tabular analysis of the gases contained in the alimentary canal has been quoted from the analyses of Jurine, Magendie, Marchand, and Chevreul, by Dr. Brinton, from whose work the above enumeration of the sources of the gas has been also taken.

Movements of the Intestines.

It remains only to consider the manner in which the food and the several secretions mingled with it are moved through the intestinal canal, so as to be slowly subjected to the influence of fresh portions of intestinal secretion, and as slowly exposed to the absorbent power of all the villi and blood-vessels of the mucous membrane. The movement of the intestines is *peristaltic*

or *vermicular*, and is effected by the alternate contractions and dilatations of successive portions of the intestinal coats. The contractions, which may commence at any point of the intestine, extend in a wave-like manner along the tube. In any given portion, the longitudinal muscular fibres contract first, or more than the circular; they draw a portion of the intestine upwards, or, as it were, backwards, over the substance to be propelled, and then the circular fibres of the same portion contracting in succession from above downwards, or, as it were, from behind forwards, press on the substance into the portion next below, in which at once the same succession of actions next ensues. These movements take place slowly, and, in health, are commonly unperceived by the mind; but they are perceptible when they are accelerated under the influence of any irritant.

The movements of the intestines are sometimes retrograde; and there is no hindrance to the backward movement of the contents of the small intestine. But almost complete security is afforded against the passage of the contents of the large into the small intestine by the ileo-cæcal valve. Besides,—the orifice of communication between the ileum and cæcum (at the borders of which orifice are the folds of mucous membrane which form the valve) is encircled with muscular fibres, the contraction of which prevents the undue dilatation of the orifice.

Proceeding from above downwards, the muscular fibres of the large intestine become, on the whole, stronger in direct proportion to the greater strength required for the onward moving of the fæces, which are gradually becoming firmer. The greatest strength is in the rectum, at the termination of which the circular unstriped muscular fibres form a strong band called the *internal* sphincter; while an *external* sphincter muscle with striped fibres is placed rather lower down, and more externally, and holds the orifice close by a constant slight contraction under the influence of the spinal cord, an influence which can be strengthened by the exercise of the will.

Experimental irritation of the brain or cord produces no evident or constant effect on the movements of the intestines during life; yet in consequence of certain conditions of the mind

the movements are accelerated or retarded; and in paraplegia the intestines appear after a time much weakened in their power, and costiveness, with a tympanitic condition, ensues. Immediately after death, irritation of both the sympathetic and pneumo-gastric nerves, if not too strong, induces genuine peristaltic movements of the intestines. Violent irritation stops the movements. These stimuli act, no doubt, not directly on the muscular tissue of the intestine, but on the ganglionic plexus before referred to.

Influence of the Nervous System on Intestinal Digestion.

As in the case of the œsophagus and stomach, the peristaltic movements of the intestines are directly due to reflex action through the ganglia and nerve fibres distributed so abundantly in their walls (p. 323); the presence of chyme acting as the stimulus, and few or no movements occurring when the intestines are empty.

The intestines are, moreover, connected with the higher nerve-centres by the splanchnic nerves, as well as other branches of the sympathetic which come to them from the cœliac and other abdominal plexuses.

The splanchnic nerves are in relation to the intestinal movements, inhibitory—these being retarded or stopped when the splanchnics are irritated. As the vasomotor nerves of the intestines, the splanchnics are also much concerned in intestinal digestion.

CHAPTER XI.

ABSORPTION.

The process of absorption has, for one of its objects, the introduction into the blood of fresh materials from the food and air, and of whatever comes into contact with the external or internal surfaces of the body; and, for another, the taking away of parts of the body itself, when, having fulfilled their office, or otherwise requiring removal, they need to be renewed. In both these

offices, *i.e.*, in both absorption from without and absorption from within, the process manifests some variety, and a very wide range of action; and in both two sets of vessels are, or may be, concerned, namely, the *blood-vessels*, and the lymph-vessels or *lymphatics*, to which the term absorbents has been also applied.

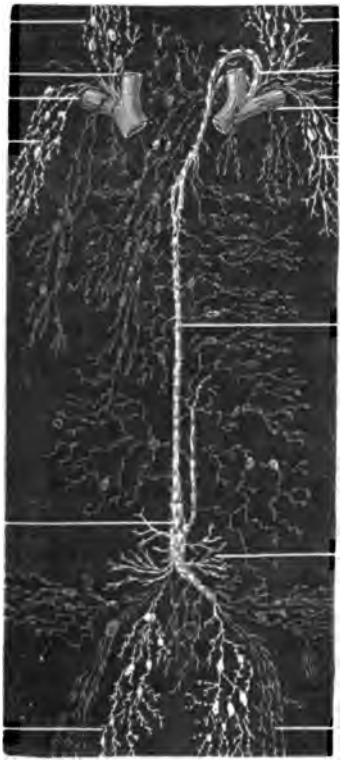
Structure and Office of the Lacteal and Lymphatic Vessels and Glands.

Besides the system of arteries and veins, with their intermediate vessels, the capillaries, there is another system of canals in man and other vertebrata, called the *lymphatic* system, which contains a fluid called *lymph*. Both these systems of vessels are concerned in absorption.

The principal vessels of the lymphatic system are, in structure and general appearance, like very small and thin-walled veins, and like them are provided with valves. By one extremity they commence by fine microscopic branches, the *lymphatic capillaries* or *lymph capillaries*, in the organs and tissues of nearly every part of the body, and by their other extremities they end directly or indirectly in two trunks which open into the large veins near the heart (fig. 172). Their contents, the *lymph* and *chyle*, unlike the blood, pass only in one direction, namely, from the fine branches to the trunk and so to the large veins, on entering which they are mingled with the stream of blood, and form part of its constituents. Remembering the course of the fluid in the lymphatic vessels, viz., its passage in the direction only *towards* the large veins in the neighbourhood of the heart, it will readily be seen from fig. 172 that the greater part of the contents of the lymphatic system of vessels passes through a comparatively large trunk called the *thoracic duct*, which finally empties its contents into the blood-stream, at the junction of the internal jugular and subclavian veins of the *left* side. There is a smaller duct on the *right* side. The lymphatic vessels of the intestinal canal are called *lacteals*, because, during digestion, the fluid contained in them resembles milk in appearance; and the *lymph* in the lacteals during the period of digestion is called *chyle*. There is no essential distinction, however, between *lacteals* and *lymphatics*.

In some parts of their course all lymphatic vessels pass through certain bodies called *lymphatic glands.*

Fig. 172.*



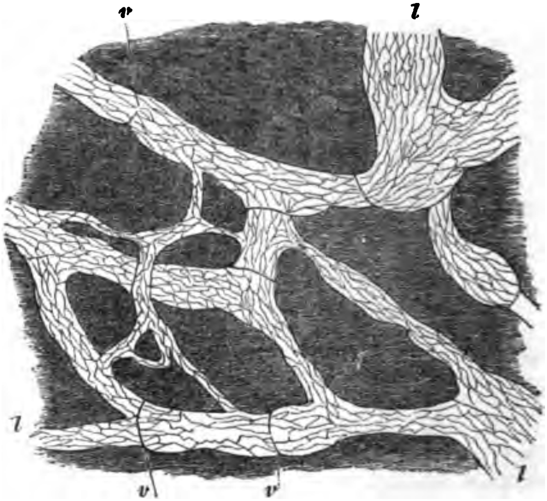
Lymphatic vessels are distributed in nearly all parts of the body. Their existence, however, has not yet been determined in the placenta, the umbilical cord, the membranes of the ovum, or in any of the non-vascular parts, as the nails, cuticle, hair and the like.

The lymphatic *capillaries* commence most commonly either in closely-meshed networks, or in irregular lacunar spaces between the various structures of which the different organs are composed.

* Fig. 172. Diagram of the principal groups of lymphatic vessels (from Quain).

Such irregular spaces, forming what is now termed the *lymph-canalicular system*, have been shown to exist in many tissues. In serous membranes such as the omentum and mesentery they occur as a connected system of very irregular branched spaces partly occupied by connective tissue-corpuscles, and both in these and in many other tissues are found to communicate freely with regular lymphatic vessels.

Fig. 173.*



In many cases, though they are formed mostly by the chinks and crannies between the blood-vessels, secreting ducts, and other parts which may happen to form the framework of the organ in which they exist, they are lined by a distinct layer of endothelium.

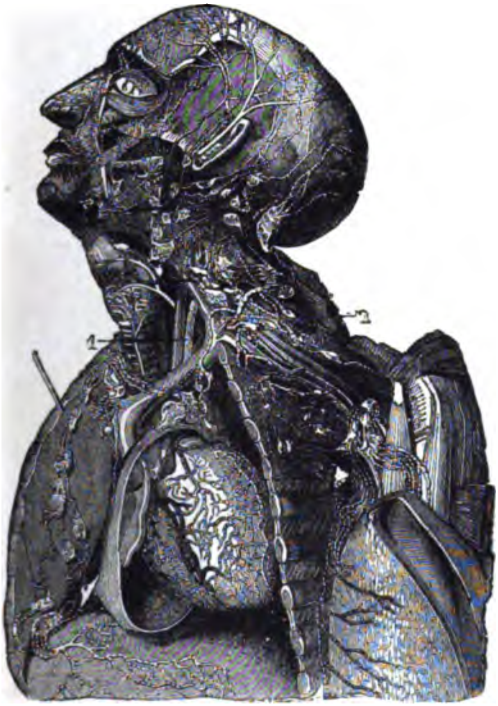
The structure of lymphatic *capillaries* is very similar to that of blood-capillaries: their walls consist of a single layer of endothelial cells of an elongated form and sinuous outline, which cohere along their edges to form a delicate membrane. They

* Fig. 173. Lymphatics of central tendon of rabbit's diaphragm, stained with nitrate of silver. The ground substance has been shaded diagrammatically to bring out the lymphatics clearly. *l*. Lymphatics lined by long narrow endothelial cells, and showing *v*. valves at frequent intervals (Schofield).

differ from blood capillaries mainly in their larger and very variable calibre, and in their numerous communications with the spaces of the *lymph-canalicular system*.

The lacteals appear to offer an illustration of another mode of origin, namely, in blind dilated extremities (figs. 159, 160); but

Fig. 174.*



* Fig. 174. Lymphatic vessels of the head and neck and the upper part of the trunk (Mascagni). $\frac{1}{6}$.—The chest and pericardium have been opened on the left side, and the left mamma detached and thrown outwards over the left arm, so as to expose a great part of its deep surface. The principal lymphatic vessels and glands are shown on the side of the head and face, and in the neck, axilla, and mediastinum. Between the left internal jugular vein and the common carotid artery, the upper ascending part of the thoracic duct marked 1, and above this, and descending to 2, the arch and last part of the duct. The termination of the upper lymphatics of the diaphragm in the mediastinal glands, as well as the cardiac and the deep mammary lymphatics, are also shown.

there is no essential difference in structure between these and the lymphatic capillaries of other parts.

Fig. 175.*

Fig. 176.†

* Fig. 175. Superficial lymphatics of the forearm and palm of the hand, $\frac{1}{3}$ (Mascagni). 5. Two small glands at the bend of the arm. 6. Radial lymphatic vessels. 7. Ulnar lymphatic vessels. 8, 8. Palmar arch of lymphatics. 9, 9′. Outer and inner sets of vessels. *b.* Cephalic vein. *d.* Radial vein. *e.* Median vein. *f.* Ulnar vein. The lymphatics are represented as lying on the deep fascia.

† Fig. 176. Superficial lymphatics of right groin and upper part of thigh, $\frac{1}{3}$ (Mascagni). 1. Upper inguinal glands. 2′. Lower inguinal or femoral glands. 3, 3. Plexus of lymphatics in the course of the long saphenous vein.

Recent discoveries seem likely to put an end soon to the long-standing discussion whether any direct communications exist between the lymph-capillaries and blood-capillaries; the need for any special intercommunicating channels seeming to disappear in the light of more accurate knowledge of the structure and endowments of the parts concerned. For while, on the one hand, the fluid part of the blood constantly exudes or is strained through the walls of the blood-capillaries, so as to moisten all the surrounding tissues, and occupy the interspaces which exist among their different elements, these same interspaces have been shown, as just stated, to form the beginnings of the lymph-capillaries. And while, for many years, the notion of the existence of any such channels between the blood-vessels and lymph-vessels, as would admit blood-corpuscles, has been given up, recent observations have proved that, for the passage of such corpuscles, it is not necessary to assume the presence of any special channels at all, inasmuch as blood-corpuscles can pass bodily, without much difficulty, through the walls of the blood-capillaries and small veins (p. 197), and could pass with still less trouble, probably, through the comparatively ill-defined walls of the capillaries which contain lymph.

It is worthy of note that, in many animals, both arteries and veins, especially the latter, are often found to be more or less completely ensheathed in large lymphatic channels. In turtles, crocodiles, and many other animals, the abdominal aorta is enclosed in a large lymphatic vessel.

Observations of Recklinghausen have led to the discovery that in certain parts of the body openings exist by which lymphatic capillaries directly communicate with parts hitherto supposed to be closed cavities. If the peritoneal cavity be injected with milk, an injection is obtained of the plexus of lymphatic vessels of the central tendon of the diaphragm (fig. 173); and on removing a small portion of the central tendon, with its peritoneal surface uninjured, and examining the process of absorption under the microscope, Recklinghausen noticed that the milk-globules ran towards small natural openings or *stomata* between the epithelial cells, and disappeared by passing vortex-like through them. The *stomata*, which have a roundish outline, are only wide

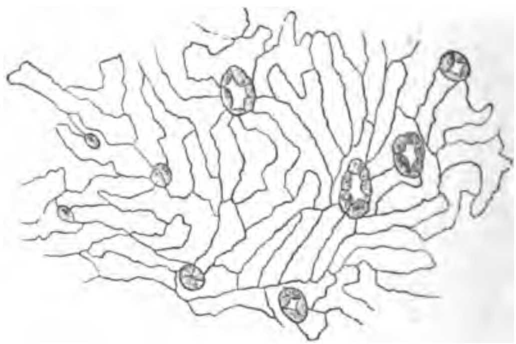
enough to admit two or three milk-globules abreast, and never exceed the size of an epithelial cell.

The stomata on the peritoneal surface of the diaphragm are the openings of short vertical canals which lead up into the lymphatics, and are lined by cells like those of germinating endothelium (p. 62).

By introducing a solution of Berlin blue into the peritoneal cavity of an animal shortly after death, and suspending it, head downwards, an injection of the lymphatic vessels of the diaphragm, through the stomata on its peritoneal surface, may readily be obtained, if artificial respiration be carried on for about half an hour. In this way it has been found that in the rabbit the lymphatics are arranged between the tendon bundles of the centrum tendineum; and they are hence termed *interfascicular*. The centrum tendineum is coated by endothelium on its pleural and peritoneal surfaces, and its substance consists of tendon bundles arranged in concentric rings towards the pleural side and in radiating bundles towards the peritoneal side.

The lymphatics of the anterior half of the diaphragm open into those of the anterior mediastinum, while those of the posterior half pass into a lymphatic vessel in the posterior mediastinum, which soon enters the thoracic duct.

Fig. 177.*



Both these sets of vessels, and the glands into which they pass, are readily injected by the method above described; and there can be little doubt that during life the flow of lymph along these channels is chiefly caused by the action of the diaphragm during respiration. As it descends in inspiration, the spaces between the *radiating* tendon bundles dilate, and lymph is sucked from the peritoneal cavity, through the widely open stomata, into the interfascicular lymphatics. During expiration, the spaces between the *concentric* tendon bundles dilate, and the lymph is squeezed into the lymphatics towards the pleural surface (Klein).

* Fig. 177. Peritoneal surface of septum cisternæ lymphaticæ magnæ of frog. The stomata, some of which are open, some collapsed, are surrounded by germinating endothelium (Klein). × 160.

It thus appears probable that during health there is a continued sucking in of lymph from the peritoneum into the lymphatics by the "pumping" action of the diaphragm; and there is doubtless an equally continuous exudation of fluid from the general serous surface of the peritoneum. When this balance of transudation and absorption is disturbed, either by increased transudation or some impediment to absorption, an accumulation of fluid necessarily takes place (ascites).

Stomata have been found by Dybskowsky in the pleura; and as they may be presumed to exist in other serous membranes, it would seem as if the serous cavities, hitherto supposed closed, form but a large lymph-sinus or widening out, so to speak, of the lymph-capillary system with which they directly communicate.

In structure, the medium-sized and larger lymphatic vessels are very like veins; having, according to Kölliker, an external coat of fibro-cellular tissue, with elastic filaments; within this, a thin layer of fibro-cellular tissue, with plain muscular fibres, which have, principally, a circular direction, and are much more abundant in the small than in the larger vessels; and again, within this, an inner elastic layer of longitudinal fibres, and a lining of epithelium; and numerous valves. The valves, constructed like those of veins, and with the free edges turned towards the heart, are usually arranged in pairs, and, in the small vessels, are so closely placed, that when the vessels are full, the valves constricting them where their edges are attached, give them a peculiar beaded or knotted appearance (fig. 179).

With the help of the valvular mechanism all occasional pressure on the exterior of the lymphatic and lacteal vessels propels the lymph towards the heart: thus muscular and other external pressure accelerates the flow of the lymph as it does that of the blood in the veins (see p. 203). The actions of the muscular fibres of the small intestine, and probably the layer of organic muscle present in each intestinal villus (p. 332), seem to assist in propelling the chyle: for, in the small intestine of a mouse, Poiseuille saw the chyle moving with intermittent propulsions that appeared to correspond with the peristaltic movements of the intestine. But for the general propulsion of the lymph and chyle, it is probable that, together with the *vis a tergo*

resulting from absorption (as in the ascent of sap in a tree,) and from external pressure, some of the force may be derived from the contractility of the vessel's own walls.

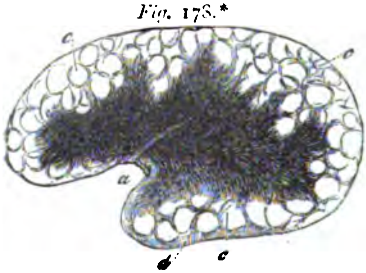
Kölliker, after watching the lymphatics in the transparent tail of the tadpole, states that no distinct movements of their walls can ever be seen, but as they are emptied after death they gradually contract, and then, after some time, again dilate to their former size, exactly as the small arteries do under the like circumstances. Thus, also, the larger vessels in the human subject commonly empty themselves after death; so that, although absorption is probably usually going on just before the time of death, it is not common to see the lymphatic or lacteal vessels full. Their power of contraction under the influence of stimuli has been demonstrated by Kölliker, who applied the wire of an electro-magnetic apparatus to some well-filled lymphatics on the skin of a boy's foot, just after the removal of his leg by amputation, and noticed that the calibre of the vessels diminished at least one half. It is most probable that this contraction of the vessels occurs during life, and that it consists, not in peristaltic or undulatory movements, but in an uniform contraction of the successive portions of the vessels, by which pressure is steadily exercised upon their contents, and which alternates with their relaxation.

Lymphatic Glands.

Almost all lymphatic and lacteal vessels in some part of their course pass through one or more small bodies called lymphatic glands (fig. 178).

A lymphatic gland is covered externally by a capsule of connective tissue, which invests and supports the glandular structure within; while prolonged from its inner surface are processes or *trabeculæ* which, entering the gland from all sides, and freely communicating, form a fibrous scaffolding or *stroma* in all parts of the interior. Thus are formed in the outer or *cortical* part of the gland (fig. 178) in the intervals of the trabeculæ, certain intercommunicating spaces termed *alveoli;*

Fig. 178.*



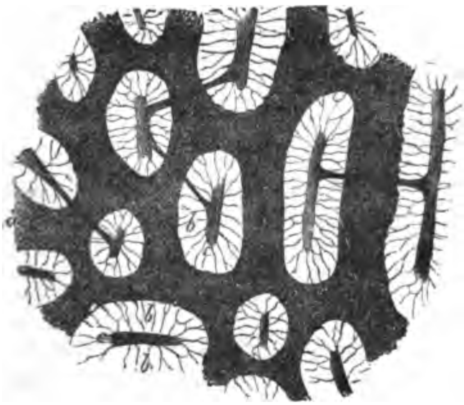
* Fig. 178. Section of a mesenteric gland from the ox, slightly magnified. *a*, hilus; *b* (in the central part of the figure), medullary substance; *c*, cortical substance with indistinct alveoli; *d*, capsule (Kölliker).

while a finer meshwork is formed in the more central or *medullary* part. In the alveoli and the trabecular meshwork the proper gland substance is contained; in the form of nodules in the cortical alveoli, and of rounded cords in the medullary part (fig. 180). The gland-substance of one part is continuous directly or indirectly with that of all others.

The essential structure of lymphatic-gland substance resembles that which was described as existing, in a simple form, in the interior of the solitary and agminated intestinal follicles (p. 327). Pervading all parts of it, and occupying the alveoli and trabecular spaces before referred to, is a network of the variety of connective tissue termed *retiform* tissue (fig. 147), the interspaces of which are occupied by lymph-corpuscles. The corpuscles are arranged in such a way, that while in the centre of the alveoli and of each mesh they are so crowded together as to

Fig. 179.*

Fig. 180.†



* Fig. 179. A lymphatic gland from the axilla, with its afferent and efferent vessels, injected with mercury (Bendz).

† Fig. 180. Section of medullary substance of an inguinal gland of an ox, *a*, *a*, glandular substance or pulp forming rounded cords joining in a continuous net (dark in the figure); *c*, *c*, trabeculæ; the space, *b*, *b*, between these and the glandular substance is the lymph-sinus, washed clear of corpuscles and traversed by filaments of retiform connective tissue (Kölliker). × 90.

be, with the retiform tissue pervading them, a consistent gland-pulp, continuous in the form of the nodules and cords, before referred to, throughout the whole gland, they are in comparatively small numbers in the outer part of the alveoli and meshes, and leave this portion, as it were, open. (See fig. 180.) This free space between the gland-pulp and the trabecular *stroma*, occupied only by retiform tissue, is called the *lymph-channel* or *lymph-path*, because it is traversed by the lymph, which is continually brought to the gland and conveyed away from it by lymphatic vessels; those which bring it being termed *afferent* vessels, and those which take it away *efferent* vessels (fig. 179).

The former enter the cortical part of the gland and open into its alveoli, at the same time that they lay aside all their coats except the epithelial lining, which may be said to continue to line the lymph-path into which the contents of the afferent vessels now pass. The *efferent* vessels begin in the *medullary* part of the gland, and are continuous with the lymph-path here as the *afferent* vessels were with the *cortical* portion; the epithelium of one is continuous with that of the other.

Blood-vessels are freely distributed to the trabecular tissue and to the gland-pulp (fig. 181).

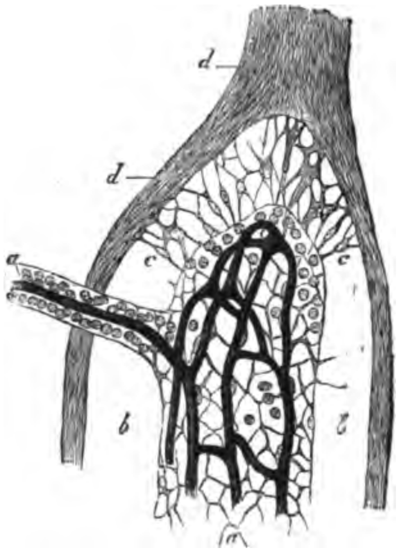
The tonsils, the pharyngeal tonsils of Kölliker, and Peyer's glands of the intestine, are really lymphatic glands, and doubtless discharge similar functions.

Properties of Lymph and Chyle.

The fluid, or *lymph*, contained in the lymphatic vessels is, under ordinary circumstances, clear, transparent, and colourless, or of a pale yellow tint. It is devoid of smell, is slightly alkaline, and has a saline taste. As seen with the microscope in the small transparent vessels of the tail of the tadpole, the lymph usually contains no corpuscles or particles of any kind; and it is probably only in the larger trunks in which, by a process similar to that to be described in the chyle, the lymph is more elaborated, that any corpuscles are formed. These corpuscles are similar to those in the chyle, but less numerous.

The fluid in which the corpuscles float is commonly and in health albuminous, and contains no fatty particles or molecular base; but it is liable to variations according to the general state of the blood, and that of the organ from which the lymph is derived As it advances towards the thoracic duct, and passes through the lymphatic glands, it becomes, like chyle, spontaneously coagulable from the formation of fibrin, and the number of corpuscles is much increased.

Fig. 181.*



The fluid contained in the *lacteals*, or lymphatic vessels of the intestine, is clear and transparent during fasting, and differs in no respect from ordinary lymph; but during digestion, it becomes milky, and is termed *chyle*.

Chyle is an opaque, whitish fluid, resembling milk in appearance, and having a neutral or slightly alkaline reaction. Its whiteness and opacity are due to the presence of innumerable particles of oily or fatty matter, of exceedingly minute though nearly uniform size, measuring on the average about $\frac{1}{30000}$ of an inch (Gulliver). These constitute what Mr. Gulliver appropriately terms the *molecular base* of chyle. Their number, and consequently the opacity of the chyle, are dependent upon the

* Fig. 181. A small portion of medullary substance from a mesenteric gland of the ox. *d*, *d*, trabeculæ; *a*, part of a cord of glandular substances from which all but a few of the lymph-corpuscles have been washed out to show its supporting meshwork of retiform tissue and its capillary blood-vessels (which have been injected, and are dark in the figure); *b*, *b*, lymph-sinus, of which the retiform tissue is represented only at *c*, *c* (Kölliker). × 300.

quantity of fatty matter contained in the food. Hence, as a rule, the chyle is whitish and most turbid in carnivorous animals; less so in herbivora; while in birds it is usually transparent. The fatty nature of the molecules is made manifest by their solubility in ether, and, when the ether evaporates, by their being deposited in various-sized drops of oil.* Yet, since they do not run together and form a larger drop, as particles of oil would, it appears very probable that each molecule consists of oil coated over with albumen, in the manner in which, as Ascherson observed, oil always becomes covered when set free in minute drops in an albuminous solution. And this view is supported by the fact, that when water or dilute acetic acid is added to chyle, many of the molecules are lost sight of, and oil-drops appear in their place, as if the investments of the molecules had been dissolved, and their oily contents had run together.

Except these molecules, the chyle taken from the villi or from lacteals near them, contains no other solid or organized bodies. The fluid in which the molecules float is albuminous, and does not spontaneously coagulate, though coagulable by the addition of ether. But as the chyle passes on towards the thoracic duct, and especially while it traverses one or more of the mesenteric glands (propelled by forces which have been described with the structure of the vessels), it is elaborated. The quantity of molecules and oily particles gradually diminishes; cells, to which the name of chyle-corpuscles is given, are developed in it; and by the formation of fibrin, it acquires the property of coagulating spontaneously. The higher in the thoracic duct the chyle advances, the more is it, in all these respects, developed; the greater is the number of chyle-corpuscles, and the larger and firmer is the clot which forms in it when withdrawn and left at rest. Such a clot is like one of blood, without the red corpuscles, having the chyle-corpuscles entangled in it, and the fatty matter forming a white creamy film on the surface of the serum. But the clot of chyle is softer and moister than that of blood. Like blood,

* Some of the molecules may remain undissolved by the ether; but this appears to be due to their being defended from the action of the ether by being entangled within the albumen which it coagulates.

also, the chyle often remains for a long time in its vessels without coagulating, but coagulates rapidly on being removed from them (Bouisson). The existence of fibrin, or of the materials which, by their union form it (p. 105 *et seq.*), is, therefore, certain; and its increase appears to be commensurate with that of the corpuscles.

The structure of the chyle-corpuscles was described when speaking of the white corpuscles of the blood, with which they are identical.

From what has been said, it will appear that perfect chyle and lymph are, in essential characters, nearly similar, and scarcely differ, except in the preponderance of fatty matter in the chyle. The comparative analysis of the two fluids obtained from the lacteals and the lymphatics of a donkey is thus given by Dr. Owen Rees:—

	Chyle.	Lymph.
Water	90·237	96·536
Albumen	3·516	1·200
Fibrin	0·370	0·120
Animal extractive	1·565	1·559
Fatty matter	3·601	a trace.
Salts	0·711	0·585
	100·000	100·000

The analyses of Nasse afford an estimate of the relative compositions of the lymph, chyle, and blood of the horse.*

	Lymph.	Chyle.	Blood.
Water	950·	935·	810·
Corpuscles		4·	92·8
Albumen	39·11	31·	80·
Fibrin		0·75	2·8
Extractive matter	4·88	6·25	5·2
Fatty matter	0·09	15·	1·55
Alkaline salts	5·61	7·	6·7
Phosphate of calcium and magnesium, oxide of iron, etc.	0·31	1·	0·95
	1000·	1000·	1000·

* The analysis of the blood differs rather widely from that given at page 109; but if it be erroneous, it is probable that corresponding errors exist in the analysis of the lymph and chyle; and that therefore the tables in the text may represent accurately enough the relation in which the three fluids stand to each other.

The contents of the thoracic duct, including both the lymph and chyle mixed, in an executed criminal, were examined by Dr. Rees, who found them to consist of—

Water	90·48
Albumen and fibrin	7·08
Extractive matter	0·108
Fatty matter	0·92
Saline matter	0·44

From all these analyses of lymph and chyle, it appears that they contain essentially the same constituents that are found in the blood. Their composition, as will be seen from the foregoing tabular statement, differs from that of the blood in degree rather than in kind; but this is no more than might be foretold from the conditions of their absorption (pp. 375, 386).

In one of Magendie's experiments, half an ounce of chyle was collected in five minutes from the thoracic duct of a middle-sized-dog; Coilard de Martigny obtained nine grains of lymph, in ten minutes, from the thoracic duct of a rabbit which had taken no food for twenty-four hours; and Gieger, from three to five pounds of lymph daily from the foot of a horse, from whom the same quantity had been flowing several years without injury to health. Bidder found, on opening the thoracic duct in cats, immediately after death, that the mingled lymph and chyle continued to flow from one to six minutes; and, from the quantity thus obtained, he estimated that if the contents of the thoracic duct continued to move at the same rate, the quantity which would pass into a cat's blood in twenty-four hours would be equal to about one-sixth of the weight of the whole body. And, since the estimated weight of the blood in cats is to the weight of their bodies as 1·7, the quantity of lymph daily traversing the thoracic duct would appear to be about equal to the quantity of blood at any time contained in the animals. Schmidt's observations on foals have yielded very similar results. By another series of experiments, Bidder estimated that the quantity of lymph traversing the thoracic duct of a dog in twenty-four hours is about equal to two-thirds of the blood in the body.

Absorption by the Lacteal Vessels.

During the passage of the chyme along the whole tract of the intestinal canal, its completely digested parts are absorbed by the blood-vessels and lacteals distributed in the mucous membrane. The blood-vessels appear to absorb chiefly the dissolved portions of the food, and these, including especially the albuminous and saccharine, they imbibe without choice; whatever can

mix with the blood passes into the vessels, as will be presently described. But the lacteals appear to absorb only certain constituents of the food, including particularly the fatty portions. The absorption by both sets of vessels is carried on most actively but not exclusively, in the villi of the small intestine; for in these minute processes, both the capillary blood-vessels and the lacteals are brought almost into contact with the intestinal contents.

It has been already stated that the villi of the small intestine (figs. 158 and 159), are minute vascular processes of mucous membrane, each containing a delicate network of blood-vessels and one or more lacteals, and are invested by a sheath of cylindrical epithelium. In the interspaces of the mucous membrane between the villi, as well as over all the rest of the intestinal canal, the lacteals and blood-vessels are also densely distributed in a close network, the lacteals, however, being more sparingly supplied to the large than to the small intestine.

There seems to be no doubt that absorption of fatty matters during digestion, from the contents of the intestines, is effected chiefly by the epithelial cells which line the intestinal tract, and especially by those which clothe the surface of the villi (fig. 158). From these epithelial cells, again, the fatty particles are passed on into the interior of the lacteal vessels (figs. 159 and 160), but how they pass, and what laws govern their so doing, are not at present exactly known.

The process of absorption by the epithelial cells, is assisted by the pressure exercised on the contents of the intestines by their contractile walls; and the absorption of fatty particles is also facilitated by the presence of the bile, and the pancreatic and intestinal secretions, which moisten the absorbing surface. For it has been found by experiment, that the passage of oil through an animal membrane is made much easier when the latter is impregnated with an alkaline fluid.

Absorption by the Lymphatic Vessels.

The real source of the lymph, and the mode in which its absorption is effected by the lymphatic vessels, were long matters

of discussion. But the problem has been much simplified by more accurate knowledge of the anatomical relations of the lymphatic capillaries. The lymph is, without doubt, identical in great part, with the *liquor sanguinis*, which, as before remarked, is always exuding from the blood-capillaries into the interstices of the tissues in which they lie; and changes in the character of the lymph correspond very closely with changes in the character of either the whole mass of blood, or of that in the vessels of the part from which the lymph is exuded. Thus Herbst found that the coagulability of the lymph is directly proportionate to that of the blood; and that when fluids are injected into the blood-vessels in sufficient quantity to distend them, the injected substance may be almost directly afterwards found in the lymphatics.

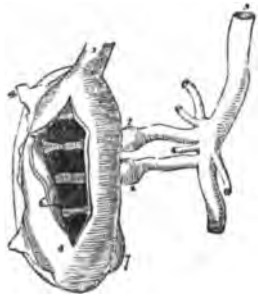
Some other matters than those originally contained in the exuded liquor sanguinis may, however, find their way with it into the lymphatic vessels. Parts which having entered into the composition of a tissue, and, having fulfilled their purpose, require to be removed, may not be altogether excrementitious, but may admit of being re-organised and adapted again for nutrition; and these may be absorbed by the lymphatics, and elaborated with the other contents of the lymph in passing through the glands.

Lymph-Hearts. In reptiles and some birds, an important auxiliary to the movement of the lymph and chyle is supplied in certain muscular sacs, named *lymph-hearts* (fig. 182), and Mr. Wharton Jones has lately shown that the caudal heart of the eel is a lymph-heart also. The number and position of these organs vary. In frogs and toads there are usually four, two anterior and two posterior; in the frog, the posterior lymph-heart on each side is situated in the ischiatic region, just beneath the skin; the anterior lies deeper, just over the transverse process of the third vertebra. Into each of these cavities several lymphatics open, the orifices of the vessels being guarded by valves, which prevent the retrograde passage of the lymph. From each heart a single vein proceeds and conveys the lymph directly into the venous system. In the frog, the inferior lymphatic heart, on each side, pours its lymph into a branch of the ischiatic vein; by the superior, the lymph is forced into a branch of the jugular vein, which issues from its anterior surface, and which becomes turgid each time that the sac contracts. Blood is prevented from passing from the vein into the lymphatic heart by a valve at its orifice.

The muscular coat of these hearts is of variable thickness; in some cases

it can only be discovered by means of the microscope; but in every case it is composed of transversely-striated fibres. The contractions of the hearts are rhythmical, occurring about sixty times in a minute, slowly, and, in comparison with those of the blood-hearts, feebly. The pulsations of the cervical pair are not always synchronous with those of the pair in the ischiatic region, and even the corresponding sacs of opposite sides are not always synchronous in their action.

Fig. 182.*



Unlike the contractions of the blood-heart, those of the lymph-heart appear to be directly dependent upon a certain limited portion of the spinal cord. For Volkmann found that so long as the portion of spinal cord corresponding to the third vertebra of the frog was uninjured, the cervical pair of lymphatic hearts continued pulsating after all the rest of the spinal cord and the brain were destroyed; while destruction of this portion, even though all other parts of the nervous centres were uninjured, instantly arrested the heart s movements. The posterior or ischiatic pair of lymph-hearts were found to be governed, in like manner, by the portion of spinal cord corresponding to the eighth vertebra. Division of the posterior spinal roots did not arrest the movements; but division of the anterior roots caused them to cease at once.

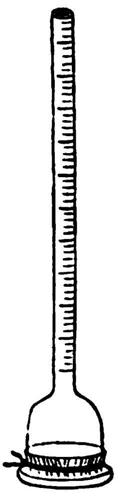
Absorption by Blood-vessels.

The process thus named is that which has been commonly called *absorption by the veins*; but the term here employed seems preferable, since, though the materials absorbed are commonly found in the veins, this is only because they are carried into them with the circulating blood, after being absorbed by all the blood-vessels (but chiefly by the capillaries) with which they were placed in contact. There is nothing in the mode of absorption by blood-vessels, or in the structure of veins, which can make the latter more active than arteries of the same size, or so active as the capillaries, in the process.

* Fig. 182. Lymphatic heart (9 lines long, 4 lines broad) of a large species of serpent, the Python bivittatus (after E. Weber). 4. The external cellular coat. 5. The thick muscular coat. Four muscular columns run across its cavity, which communicates with three lymphatics (1—only one is seen here), and with two veins (2, 2). 6. The smooth lining membrane of the cavity. 7. A small appendage, or auricle, the cavity of which is continuous with that of the rest of the organ.

In the absorption by the lymphatics or lacteal vessels just described, there appears something like the exercise of choice in the materials admitted into them. But the absorption by blood-vessels presents no such appearance of selection of materials; rather, it appears, that every substance, whether gaseous, liquid, or a soluble or minutely divided solid, may be absorbed by the blood-vessels, provided it is capable of permeating their walls, and of mixing with the blood; and that of all such substances, the mode and measure of absorption are determined solely by their physical or chemical properties and conditions, and by those of the blood and the walls of the blood-vessels.

Fig. 183.*



The phenomena are, indeed, exactly comparable to that passage of fluids through membrane, which occurs quite independently of vital conditions, and the earliest and best scientific investigation of which was made by Dutrochet. The instrument which he employed in his experiments was named an endosmometer. It may consist of a graduated tube expanded into an open-mouthed bell at one end, over which a portion of membrane is tied (fig. 183). If now the bell be filled with a solution of a salt—say chloride of sodium, and be immersed in water, the water will pass into the solution, and part of the salt will pass out into the water; the water will pass into the solution, much more rapidly than the salt will pass out into the water, and the diluted solution will rise in the tube. To this passage of fluids through membrane the term *Osmosis* is applied.

The nature of the membrane used as a septum, and its affinity for the fluids subjected to experiment have an important influence, as might be anticipated, on the rapidity and duration of the osmotic current. Thus, if a piece of ordinary bladder be used as the septum between water and alcohol, the current is almost solely from the water to the alcohol, on account of the much greater affinity of water for this kind of membrane; while, on the other hand, in the case of a membrane of caoutchouc, the

alcohol, from its greater affinity for this substance, would pass freely into the water.

Various opinions have been advanced concerning the nature of the force by which fluids of different chemical composition thus tend to mix through an intervening membrane. According to some, this power is the result of the different degrees of capillary action exerted by the pores of the membrane upon the two fluids. Prof. Graham, however, believes that the passage or osmose of water through membrane may be explained by supposing that it combines with the membranous septum, which thus becomes hydrated, and that on reaching the other side it partly leaves the membrane, which thus becomes to a certain degree de-hydrated. For example, a membrane such as that used in the endosmometer, is hydrated to a higher degree if placed in pure water than in a neutral saline solution. Hence, in the case of the endosmometer filled with the saline solution and placed in water, the equilibrium of hydration is different on the two sides; the outer surface being in contact with pure water tends to hydrate itself in a higher degree than the inner surface does. "When the full hydration of the outer surface extends through the thickness of the membrane, and reaches the inner surface, it there receives a check. The degree of hydration is lowered, and water must be given up by the inner layer of the membrane." Thus the osmose or current of water through the membrane is caused. The passage *outwards* of the saline solution, on the other hand, is not due probably to any actual *fluid* current; but to a solution of the salt in successive layers of the water contained in the pores of the membrane, until it reaches the outer surface and *diffuses* in the water there situate.

Thus, "the water movement in osmose is an affair of hydration and of de-hydration in the substance of the membrane or other colloid septum, and the diffusion of the saline solution placed within the osmometer has little or nothing to do with the osmotic result, otherwise than as it affects the state of hydration of the septum."

Prof. Graham has classed various substances according to the degree in which they possess this property of passing, when in a state of solution in water, through membrane; those which pass freely, inasmuch as they are usually capable of crystallization, being termed *crystalloids*, and those which pass with difficulty, on account of their, physically, glue-like characters, *colloids*.

A remarkable exception to the rule laid down by the separation of these groups into colloids and crystalloids is afforded by Hæmoglobin (p. 116), which is *colloid*, so far as its incapability of diffusion is concerned; while, at the same time, it is capable of crystallization.

This distinction, however, between colloids and crystalloids which is made the basis of their classification, is by no means the only difference between them. The *colloids*, besides the absence of power to assume a crystalline form, are characterised

by their inertness as acids or bases, and feebleness in all ordinary chemical relations. Examples of them are found in albumen, gelatin, starch, hydrated alumina, hydrated silicic acid, etc.; while the *crystalloids* are characterised by qualities the reverse of those just mentioned as belonging to *colloids*. Alcohol, sugar, and ordinary saline substances are examples of *crystalloids*.

Absorption by blood-vessels is the consequence of their walls being, like the membranous septum of the endosmometer, porous and capable of imbibing fluids, and of the blood being so composed that most fluids will mingle with it. The process of absorption, in an instructive, though very imperfect degree, may be observed in any portion of vascular tissue removed from the body. If such a one be placed in a vessel of water, it will shortly swell, and become heavier and moister, through the quantity of water imbibed or soaked into it; and if now, the blood contained in any of its vessels be let out, it will be found diluted with water, which has been absorbed by the blood-vessels and mingled with the blood. The water round the piece of tissue also will become blood-stained; and if all be kept at perfect rest, the stain derived from the solution of the colouring matter of the blood (together with which chemistry would detect some of the albumen and other parts of the liquor sanguinis) will spread more widely every day. The same will happen if the piece of tissue be placed in a saline solution instead of water, or in a solution of colouring or odorous matter, either of which will give their tinge or smell to the blood, and receive, in exchange, the colour of the blood.

Even so simple an experiment will illustrate the absorption by blood-vessels during life; the process it shows is imitated, but with these differences: that, during life, as soon as water or any other substance is admitted into the blood, it is carried from the place at which it was absorbed into the general current of the circulation, and that the colouring matter of the blood is not dissolved so as to ooze out of the blood-vessels into the fluid which they are absorbing.

The absorption of gases by the blood may be thus simply imitated. If venous blood be suspended in a moist bladder in

the air, its surface will be reddened by the contact of oxygen, which is first dissolved in the fluid that moistens the bladder, and is then carried in the fluid to the surface of the blood: while, on the other hand, watery vapour and carbonic acid will pass through the membrane, and be exhaled into the air.

The rapidity with which matters may be absorbed from the stomach probably by the blood-vessels chiefly, and diffused through the textures of the body, may be gathered from the history of some experiments by Dr. Bence Jones. From these it appears that even in a quarter of an hour after being given on an empty stomach, chloride of lithium may be diffused into all the vascular textures of the body, and into some of the non-vascular, as the cartilage of the hip-joint, as well as into the aqueous humour of the eye. Into the outer part of the crystalline lens it may pass after a time, varying from half an hour to an hour and a half. Carbonate of lithium, when taken in five or ten grain doses on an empty stomach, may be detected in the urine in 5 or 10 minutes; or, if the stomach be full at the time of taking the dose, in 20 minutes. It may sometimes be detected in the urine, moreover, for six, seven, or even eight days.

Some experiments on the absorption of various mineral and vegetable poisons, by Mr. Savory, have brought to light the singular fact, that, in some cases, absorption takes place more rapidly from the rectum than from the stomach. Strychnia, for example, when in solution, produces its poisonous effects much more speedily when introduced into the rectum than into the stomach. When introduced in the solid form, however, it is absorbed more rapidly from the stomach than from the rectum, doubtless because of the greater solvent property of the secretion of the former than of that of the latter.

With regard to the degree of absorption by living blood-vessels, much depends on the facility with which the substance to be absorbed can penetrate the membrane or tissue which lies between it and the blood-vessels; for, naturally, the blood-vessels are not bare to absorb. Thus absorption will hardly take place through the epidermis, but is quick when the epidermis is removed, and the same vessels are covered with only the surface

of the cutis, or with granulations. In general, the absorption through membranes is in an inverse proportion to the thickness of their epithelia; so Müller found the urinary bladder of a frog traversed in less than a second; and the absorption of poisons by the stomach or lungs appears sometimes accomplished in an immeasurably small time.

The substance to be absorbed must, as a general rule, be in the liquid or gaseous state, or, if a solid, must be soluble in the fluids with which it is brought in contact. Hence the marks of tattooing, and the discoloration produced by nitrate of silver taken internally, remain. Mercury may be absorbed even in the metallic state; and in that state may pass into and remain in the blood-vessels, or be deposited from them (Oesterlen); and such substances as exceedingly finely-divided charcoal, when taken into the alimentary canal, have been found in the mesenteric veins (Oesterlen); the insoluble materials of ointments may also be rubbed into the blood-vessels; but there are no facts to determine how these various substances effect their passage. Oil, minutely divided, as in an emulsion, will pass slowly into blood-vessels, as it will through a filter moistened with water (Vogel); and, without doubt, fatty matters find their way into the blood-vessels as well as the lymph-vessels of the intestinal canal, although the latter seem to be specially intended for their absorption.

As in the experiments before referred to, the less dense the fluid to be absorbed, the more speedy, as a general rule, is its absorption by the living blood-vessels. Hence the rapid absorption of water from the stomach; also of weak saline solutions; but with strong solutions, there appears less absorption into, than effusion from, the blood-vessels.

The absorption is the less rapid the fuller and tenser the blood-vessels are; and the tension may be so great as to hinder altogether the entrance of more fluid. Thus, Magendie found that when he injected water into a dog's veins to repletion, poison was absorbed very slowly; but when he diminished the tension of the vessels by bleeding, the poison acted quickly. So, when cupping-glasses are placed over a poisoned wound,

they retard the absorption of the poison, not only by diminishing the velocity of the circulation in the part, but by filling all its vessels too full to admit more.

On the same ground, absorption is the quicker the more rapid the circulation of the blood; not because the fluid to be absorbed is more quickly imbibed into the tissues, or mingled with the blood, but because as fast as it enters the blood, it is carried away from the part, and the blood, being constantly renewed, is constantly as fit as at the first for the reception of the substance to be absorbed.

CHAPTER XII.

NUTRITION AND GROWTH.

Nutrition or nutritive assimilation is that modification of the formative process peculiar to living bodies by which tissues and organs already formed maintain their integrity. By the incorporation of fresh nutritive principles into their substance, the loss consequent on the waste and natural decay of the component particles of the tissues is repaired; and each elementary particle seems to have the power not only of attracting materials from the blood, but of causing them to assume its structure, and participate in its vital properties.

The relations between development and growth have been already stated (Chap. I.); under the head of Nutrition will be now considered the process by which parts are maintained in the same general conditions of form, size, and composition, which they have already, by development and growth, attained; and this, notwithstanding continual changes in their component particles. It is by this process that an adult person, in health, is maintained, through a series of some years, with the same general outline of features, the same size and form, and perhaps even the same weight; although, during all this time, the several portions of his body are continually changing: their particles decaying and being removed, and then replaced by the

formation of new ones, which, in their turn, also die and pass away. Neither is it only a general similarity of the whole body which is thus maintained. Every organ or part of the body, as much as the whole, maintains, speaking generally, its form and composition, as the issue of the changes continually taking place among its particles.

The change of component particles, in which the nutrition of organs consists, is most evidently shown when, in growth, they maintain their form and other general characters, but increase in size. When, for example, a long bone increases in circumference, and in the thickness of its walls, while, at the same time, its medullary cavity enlarges, it can only be by the addition of materials to its exterior, and a coincident removal of them from the interior of its wall (p. 91); and so it must be with the growth of even the minutest portions of a tissue. And that a similar change of particles takes place, even while parts retain a perfect uniformity, may be proved, if it can be shown that all the parts of the body are subject to waste and impairment.

In many parts, the removal of particles is evident. Thus, as will be shown when speaking of Secretion, the elementary structures composing glands are the parts of which the secretions are composed: each gland is constantly casting off its cells, or their contents, in the secretion which it forms: yet each gland maintains its size and proper composition, because for every cell cast off a new one is produced. So also the epidermis and all such tissues are maintained. In the muscles each act of contraction is accompanied with a change in the composition of the contracting tissue, although the change from this cause is less rapid and extensive than was once supposed. Thence, the development of heat in acting muscles, and thence the discharge of urea, carbonic acid, and water—the ordinary products of the decomposition of the animal tissues—which follows all active muscular exercise. Indeed, the researches of Helmholtz almost demonstrate the chemical change that muscles undergo after long-repeated contractions; yet the muscles retain their structure and composition, because the particles thus changed are replaced

by new ones resembling those which preceded them. So again, the increase of alkaline phosphates discharged with the urine after great mental exertion, seems to prove that the various acts of the nervous system are attended with change in the composition of the nervous tissue; yet the condition of that tissue is maintained.

But besides the impairment and change of composition to which all parts are subject in the discharge of their natural functions, an amount of impairment which will be in direct proportion to their activity, they are all liable to decay and degeneration of their particles, even while their natural actions are not called forth. It may be proved, as Dr. Carpenter first clearly showed, that every particle of the body is formed for a certain period of existence in the ordinary condition of active life; at the end of which period, if not previously destroyed by outward force or exercise, it degenerates and is absorbed, or dies and is cast out.

The simplest examples that can be adduced of this are in the hair and teeth; and it may be observed, that, in the processes involved in their decay and reproduction, all the great features of the process of nutrition seem to be represented.*

An eyelash which naturally falls, or which can be drawn out without pain, is one that has lived its natural time, and has died, and been separated from the living parts. In its bulb such an one will be found different from those that are still living in any period of their age. In the early period of the growth of a dark eyelash, the medullary substance appears like an interior cylinder of darker granular substance, continued down to the deepest part, where the hair enlarges to form the bulb. This enlargement, which is of nearly cup-like form, appears to depend on the accumulation of nucleated cells, whose nuclei, according to their position, are either, by narrowing and elongation, to form the fibrous substance of the outer part of the growing and further protruding hair, or are to be transformed into the granular matter of its medullary portion. At the time of early and most active growth, all the cells and nuclei contain abundant pigment-matter, and the whole bulb looks nearly black. The sources of the material out of which the cells form themselves are at least two; the inner surface of the sheath or capsule, which dips into the skin, enveloping the hair, and the surface of a vascular pulp which fits in a conical cavity in the bottom of the hair-bulb.

* These and other instances are related more in detail in Sir J. Paget's Lectures on Surgical Pathology, from which this chapter was originally written.

Such is the state of parts so long as the growing hair is all dark. But as the hair approaches the end of its existence, instead of the almost sudden enlargement at its bulb, it only swells a little, and then tapers nearly to a point; the conical cavity in its base is contracted; and the cells produced on the inner surface of the capsule contain no pigment. Still, for some time, it continues thus to live and grow; and the vigour of the pulp lasts rather longer than that of the sheath or capsule, for it continues to produce pigment-matter for the medullary substance of the hair after the cortical substance has become white. Thus the column of dark medullary substance appears paler and more slender, and perhaps interrupted, down to the point of the conical pulp which, though smaller, is still distinct, because of the pigment cells covering its surface.

Fig. 184.*

At length the pulp can be no longer discerned, and uncoloured cells are alone produced, and maintain the latest growth of the hair. With these it appears to grow yet some further distance; for traces of the elongation of their nuclei into fibres appear in lines running from the inner surface of the capsule inwards and along the surface of the hair; and the column of dark medullary substances ceases at some distance above the lower end of the contracted hair-bulb. The end of all is the complete closure of the conical cavity in which the hair-pulp was lodged, the cessation of the production of new cells from the inner surface of the capsule, and the detachment of the hair which, as a dead part, is separated and falls.

Such is the life of a hair, and such its death; which death is spontaneous, independent of exercise, or of any mechanical external force—the natural termination of a certain period of life. Yet, before the hair dies, provision

* Fig. 184. Intended to represent the changes undergone by a hair towards the close of its period of existence. At A, its activity of growth is diminishing, as shown by the small quantity of pigment contained in the cells of the pulp, and by the interrupted line of dark medullary substance. At B, provision is being made for the formation of a new hair, by the growth of a new pulp connected with the pulp or capsule of the old hair. C. A hair at the end of its period of life, deprived of its sheath and of the mass of cells composing the pulp of a living hair.

is made for its successor: for when its growth is failing, there appears below its base a dark spot, the germ or young pulp of the new hair covered with cells containing pigment, and often connected by a series of pigment cells with the old pulp or capsule (fig. 184).

Probably there is an intimate analogy between the process of successive life and death, and life communicated to a successor, which is here shown and that which constitutes the ordinary nutrition of a part. It may be objected, that the death and casting out of the hair cannot be imitated in internal parts; therefore, for an example in which the assumed absorption of the worn-out or degenerate internal particles is imitated in larger organs at the end of their appointed period of life, the instance of the deciduous or milk-teeth may be adduced.

Fig. 185.*

Each milk-tooth is developed from its germ; and in the course of its own development, separates a portion of itself to be the germ of its successor; and each, having reached its perfection, retains for a time its perfect state, and still lives, though it does not grow. But at length, as the new tooth comes, the deciduous tooth dies, or rather its crown dies, and is cast out like the dead hair, while its fang, with its bony sheathing, and vascular and nervous pulp, degenerates and is absorbed (fig. 185). The degeneration is accompanied by some unknown spontaneous decomposition of the fang; for it could not be absorbed unless it was first so changed as to be soluble. And it is degeneration, not death, which precedes its removal; for when a tooth-fang dies, as that of the second tooth does in old age, then it is not absorbed, but cast out entire, as a dead part.

The hair and teeth may be fairly taken as types of what occurs in other parts, for they are parts of complex organic structure and composition, and the teeth-pulps, which are absorbed as well as the fangs, are very vascular and sensitive.

Nor are they the only instances that might be adduced. The like development, persistence for a time in the perfect state, death, and discharge, appear in all the varieties of cuticles and gland-cells; and in the epidermis, as in the teeth, there is evidence of decomposition of the old cells, in the fact of the different influence which acetic acid and potash exercise on them

* Fig. 185. Section of a portion of the upper jaw of a child, showing a new tooth in process of formation, the fang of the corresponding deciduous tooth being absorbed.

and on the young cells. Seeing, then, that the process of nutrition, as thus displayed, both in active organs and in elementary cells, appears in these respects similar, the general conclusion may be that, in nutrition, the ordinary course of each complete elementary organ in the body, after the attainment of its perfect state by development and growth, is to remain in that state for a time; then, independently of the death or decay of the whole body, and in some measure, independently of its own exercise, or exposure to external violence, to die or to degenerate; and then, being cast out or absorbed, to make way for its successor.

It appears, moreover, that the length of life which each part is to enjoy is fixed and determinate, though in some degree subject to accidents and to the expenditure of life in exercise. It is not likely that all parts are made to last a certain and equal time, and then all need to be changed. The bones, for instance, when once completely formed, must last longer than the muscles and other softer tissues. But when we see that the life of certain parts is of determined length, whether they be used or not, we may assume, from analogy, the same of nearly all.

The deciduous human teeth have an appointed average duration of life. So have the deciduous teeth of all other animals; and in all the numerous instances of moulting, shedding of antlers, of desquamation, change of plumage in birds, and of hair in Mammalia, the only explanation is that these organs have their severally appointed times of living, at the ends of which they degenerate, die, are cast away, and in due time are replaced by others which, in their turn, are to be developed to perfection, to live their life in the mature state, and in their turn to be cast off. So also, in some elementary structures we may discern the same laws of determinate period of life, death, or degeneration, and replacement. They are evident in the history of the blood-corpuscles, both in the superseding of the first set of them by the second at a definite period in the life of the embryo, and in the replacement of those that degenerate by others new-formed from lymph-corpuscles (see p. 129). And if we could suppose the blood-corpuscles grouped together in a tissue instead of floating, we might have in the changes they present an image of the nutrition of the elements of the tissues.

The *duration of life in each particle* is liable to be modified; especially by the exercise of the function of the part. The less a part is exercised the longer do its component particles appear to live: the more active its functions are, the less prolonged is the existence of its individual particles. So in the case of

single cells; if the general development of the tadpole be retarded by keeping it in a cold, dark place, and if hereby the function of the blood-corpuscles be slowly and imperfectly discharged, they will maintain their embryonic state for even several weeks later than usual, the development of the second set of corpuscles will be proportionally postponed, and the individual life of the corpuscles of the first set will be, by the same time, prolonged.

The process by which a new particle is formed in the place of the old one is probably always a process of development; that is, the cell or fibre, or other element of tissue, passes in its formation through the same stages of development as those elements of the same tissue did which were first formed in the embryo. This is probable from the analogy of the hair, the teeth, the epidermis, and all the tissues that can be observed: in all, the process of repair or replacement is effected through development of the new parts. The existence of nuclei or cytoblasts in nearly all parts that are the seats of active nutrition makes the same probable. For these nuclei, such as are seen so abundant in strong, active muscles, are not remnants of the embryonic tissue, but germs or organs of power for new formation, and their abundance often appears directly proportionate to the activity of growth. Thus, they are always abundant in the fœtal tissues, and those of the young animal: and they are peculiarly numerous in the muscles and the brain, and their disappearance from a part in which they usually exist is a sure accompaniment and sign of degeneration.

A difference may be drawn between what may be called *nutritive reproduction* and *nutritive repetition.* The former is shown in the case of the human teeth. As the deciduous tooth is being developed, a part of its productive capsule is detached, and serves as a germ for the formation of the second tooth; in which second tooth, therefore, the first may be said to be reproduced, in the same sense as that in which we speak of the organs by which new individuals are formed, as the reproductive organs. But in the shark's jaws, and others, in which we see row after row of teeth succeeding each other, the row behind is not formed

of germs derived from the row before: the front row is simply repeated in the second one, the second in the third, and so on. So, in cuticle, the deepest layer of epidermis-cells derives no germs from the layer above: their development is not like a reproduction of the cells that have gone on towards the surface before them: it is only a repetition. It is not improbable that much of the difference in the degree of repair, of which the several tissues are capable after injuries or diseases, may be connected with these differences in their ordinary mode of nutrition.

In order that the process of nutrition may be perfectly accomplished, certain conditions are necessary. Of these, the most important are: 1. A right state and composition of the blood, from which the materials for nutrition are derived. 2. A regular and not far distant supply of such blood. 3. A certain influence of the nervous system. 4. A natural state of the part to be nourished.

1. This *right condition of the blood* does not necessarily imply its accordance with any known standard of composition, common to all kinds of healthy blood, but rather the existence of a certain adaptation between the blood and the tissues, and even the several portions of each tissue. Such an adaptation, peculiar to each individual, is determined in its first formation, and is maintained in the concurrent development and increase of both blood and tissues; and upon its maintenance in adult life appears to depend the continuance of a healthy process of nutrition, or, at least, the preservation of that exact sameness of the whole body and its parts, which constitutes the perfection of nutrition. Some notice of the maintenance of this sameness in the blood has been given already (p. 131), in speaking of the power of assimilation which the blood exercises, a power exactly comparable with this of maintenance by nutrition in the tissues. And evidence of the adaptation between the blood and the tissues, and of the exceeding fineness of the adjustment by which it is maintained, is afforded by the phenomena of diseases, in which, after the introduction of certain animal poisons, even in very minute quantities, the whole mass of the blood is altered in composition, and the solid tissues are perverted in their nutrition. It is necessary to refer only to such diseases as syphilis, small-pox, and other eruptive fevers, in illustration. And when the absolute dependence of all the tissues on the blood for their very existence is remembered, on the one hand, and, on the other, the rapidity with which substances introduced into the blood are diffused into all, even non-vascular textures (p. 391), it need be no source of wonder that any, even the slightest alteration from the normal constitution of the blood should be immediately reflected, so to speak, as a change in the nutrition of the solid tissues and organs which it is destined to nourish.

2. The necessity of *an adequate supply of appropriate blood in or near the part to be nourished*, in order that its nutrition may be perfect, is shown in the frequent examples of atrophy of parts to which too little blood is sent, of mortification or arrested nutrition when the supply of blood is entirely cut off, and of defective nutrition when the blood is stagnant in a part. That the nutrition of a part may be perfect, it is also necessary that the blood should be brought sufficiently near to it for the elements of the tissue to imbibe, through the walls of the blood-vessels, the nutritive materials which they require. The blood-vessels themselves take no share in the process of nutrition, except as carriers of the nutritive matter. Therefore, provided they come so near that this nutritive matter may pass by imbibition into the part to be nourished, it is comparatively immaterial whether they ramify within the substance of the tissue, or are distributed only on its surface or border.

The blood-vessels serve alike for the nutrition of the vascular and the non-vascular parts, the difference between which, in regard to nutrition, is less than it may seem. For the vascular, the nutritive fluid is carried in streams into the interior; for the non-vascular, it flows on the surface; but in both alike, the parts themselves imbibe the fluid; and although the passage through the walls of the blood-vessels may effect some change in the materials, yet all the process of formation is, in both alike, outside the vessels. Thus, in muscular tissue, the fibrils in the very centre of the fibre nourish themselves: yet these are distant from all blood-vessels, and can only by imbibition receive their nutriment. So, in bones, the spaces between the blood-vessels are wider than in muscle; yet the parts in the meshes nourish themselves, imbibing materials from the nearest source. The non-vascular epidermis, though no vessels pass into its substance, yet imbibes nutritive matter from the vessels of the immediately subjacent cutis, and maintains itself, and grows. The instances of the cornea and vitreous humour are stronger, yet similar; and sometimes even the same tissue is in one case vascular, in the other not, as the osseous tissue, which, when it is in masses or thick layers, has blood-vessels running into it; but when it is in thin layers, as in the lachrymal and turbinated bones, has not. These bones subsist on the blood flowing in the minute vessels of the mucous membrane, from which the epithelium derives nutriment on one side, the bone on the other, and the tissue of the membrane itself on every side: a striking instance how, from the same source, many tissues maintain themselves, each exercising its peculiar assimilative and self-formative power.

3. The third condition essential to a healthy nutrition, is *a certain influence of the nervous system.*

It has been held that the nervous system cannot be essential to a healthy course of nutrition, because in plants and the early embryo, and in the lowest animals, in which no nervous system is developed, nutrition goes on without it. But this is no proof that in animals which have a nervous system, nutrition may be independent of it; rather, it may be assumed, that in ascending development, as one system after another is added or increased, so the highest (and, highest of all, the nervous system) will always be inserted and blended in a more and more intimate relation with all the rest: according to the general law, that the interdependence of parts augments with their development.

The reasonableness of this assumption is proved by many facts showing

the influence of the nervous system on nutrition, and by the most striking of these facts being observed in the higher animals, and especially in man. The influence of the mind in the production, aggravation, and cure of organic diseases is matter of daily observation, and a sufficient proof of influence exercised on nutrition through the nervous system.

Independently of mental influence, injuries either to portions of the nervous centres, or to individual nerves, are frequently followed by defective nutrition of the parts supplied by the injured nerves, or deriving their nervous influence from the damaged portions of the nervous centres. Thus, lesions of the spinal cords are sometimes followed by mortification of portions of the paralysed parts; and this may take place very quickly, as in a case by Sir B. C. Brodie, in which the ankle sloughed within twenty-four hours after an injury of the spine. After such lesions also, the repair of injuries in the paralysed parts may take place less completely than in others; so, Mr. Travers mentions a case in which paraplegia was produced by fracture of the lumbar vertebræ, and, in the same accident, the humerus and tibia were fractured. The former in due time united: the latter did not. The same fact was illustrated by some experiments of Dr. Baly, in which having, in salamanders, cut off the end of the tail, and then thrust a thin wire some distance up the spinal canal, so as to destroy the cord, he found that the end of the tail was reproduced more slowly than in other salamanders in whom the spinal cord was left uninjured above the point at which the tail was amputated. Illustrations of the same kind are furnished by the several cases in which division or destruction of the trunk of the trigeminal nerve has been followed by incomplete and morbid nutrition of the corresponding side of the face; ulceration of the cornea being often directly or indirectly one of the consequences of such imperfect nutrition. Part of the wasting and slow degeneration of tissue in paralysed limbs is probably referable also to the withdrawal of nervous influence from them; though, perhaps, more is due to the want of use of the tissues.

Undue irritation of the trunks of nerves, as well as their division or destruction, is sometimes followed by defective or morbid nutrition. To this may be referred the cases in which ulceration of the parts supplied by the irritated nerves occurs frequently, and continues so long as the irritation lasts. Further evidence of the influence of the nervous system upon nutrition is furnished by those cases in which, from mental anguish, or in severe neuralgic headaches, the hair becomes grey very quickly, or even in a few hours.

So many and various facts leave little doubt that the nervous system exercises an influence over nutrition as over other organic processes; and they cannot be easily explained by supposing that the changes in the nutritive processes are only due to the variations in the size of the blood-vessels supplying the affected parts, although this is, doubtless, one important element in producing the result.

The question remains, through what class of nerves is the influence exerted? When defective nutrition occurs in parts rendered inactive by injury of the motor nerve alone, as in the muscles and other tissues of a paralysed face or limb, it may appear as if the atrophy were the direct consequence of the loss of power in the motor nerves; but it is more probable that the atrophy is the consequence of the want of exercise of the parts; for if the muscles be

exercised by artificial irritation of their nerves their nutrition will be less defective (J. Reid). The defect of the nutritive process which ensues in the face and other parts, however, in consequence of destruction of the trigeminal nerve, cannot be referred to loss of influence of any motor nerves; for the motor-nerves of the face and eye, as well as the olfactory and optic, have no share in the defective nutrition which follows injury of the trigeminal nerve; and one or all of them may be destroyed without any direct disturbance of the nutrition of the parts they severally supply.

It must be concluded, therefore, that the influence which is exercised by nerves over the nutrition of parts to which they are distributed is to be referred, in part or altogether, either to the nerves of common sensation, or to the vaso-motor nerves, or, as it is by some supposed, to nerve-fibres (*trophic* nerves), which preside specially over the nutrition of the tissues and organs to which they are supplied (see Chapter on the Nervous System).

It is not at present possible to say whether the influence on nutrition is exercised through the cerebro-spinal or through the sympathetic nerves, which, in the parts on which the observation has been made, are generally combined in the same sheath. The truth perhaps is, that it may be exerted through either or both of these nerves. The defect of nutrition which ensues after lesion of the spinal cord alone, the sympathetic nerves being uninjured, and the general atrophy which sometimes occurs in consequence of diseases of the brain, seem to prove the influence of the cerebro-spinal system: while the observation of Magendie and Mayer, that inflammation of the eye is a constant result of ligature of the sympathetic nerve in the neck, and many other observations of a similar kind, exhibit very well the influence of the latter nerve in nutrition.

4. The fourth condition necessary to healthy nutrition is *a healthy state of the part to be nourished.* This seems proved by the very nature of the process, which consists in the formation of new parts like those already existing; for, unless the latter are healthy, the former cannot be so. Whatever be the condition of a part, it is apt to be perpetuated by assimilating exactly to itself, and endowing with all its peculiarities, the new particles which it forms to replace those that degenerate. So long as a part is healthy, and the other conditions of healthy nutrition exist, it maintains its healthy condition. But, according to the same law, if the structure of a part be diseased or in any way altered from its natural condition, the alteration is maintained; the altered, like the healthy structure, is perpetuated.

The same exactness of the assimilation of the new parts to the old, which is seen in the nutrition of the healthy tissues, may be observed also in those that are formed in disease. By it, the exact form and relative size of a cicatrix are preserved from year to year; by it, the thickening and induration to which inflammation gives rise are kept up, and the various morbid states of the blood in struma, syphilis, and other chronic diseases are maintained, notwithstanding all diversities of diet. By this precision of the assimilating process, may be explained the law that certain diseases occur only once in the same person, and that certain others are apt to recur frequently; because in both cases alike, the alteration produced by the first attack of the disease is maintained by the exact likeness which the new parts bear to the old ones.

The period, however, during which an alteration of structure may be

exactly maintained by nutrition, is not unlimited; for in nearly all altered parts there appears to exist a tendency to recover the perfect state; and, in many cases, this state is, in time, attained. To this we may attribute the possibility of revaccination after the lapse of some years; the occasional recurrence of small-pox, scarlet-fever, and the like diseases, in the same person; the wearing out of scars, and the complete restoration of tissues that have been altered by injury or disease.

Such are some of the more important conditions which appear to be essential to healthy nutrition. Absence or defect of any one of them is liable to be followed by disarrangement of the process; and the various diseases resulting from defective nutrition appear to be due to the failure of these conditions, more often than to imperfection of the process itself.

GROWTH.

Growth, as has been already observed, consists in the increase of a part in bulk and weight by the addition to its substance of particles similar to its own, but more than sufficient to replace those which it loses by the waste or natural decay of its tissue. The structure and composition of the part remain the same; but the increase of healthy tissue which it receives is attended with the capability of discharging a larger amount of its ordinary function.

While development is in progress, growth frequently proceeds with it in the same part, as in the formation of the various organs and tissues of the embryo, in which parts, while they grow larger, are also gradually more developed until they attain their perfect state. But, commonly, growth continues after development is completed, and in some parts, continues even after the full stature of the body is attained, and after nearly every portion of it has gained its perfect state in both size and composition.

In certain conditions, this continuance or a renewal of growth may be observed in nearly every part of the body. When parts have attained the full size which in the ordinary process of growth they reach, and are then kept in a moderate exercise of their functions, they commonly (as already stated) retain almost exactly the same dimensions through the adult period of life.

But when, from any cause, a part already full-grown in proportion to the rest of the body, is called upon to discharge an unusual amount of its ordinary function, the demand is met by a corresponding increase or growth of the part. Illustrations of this are afforded by the increased thickening of cuticle at parts where it is subjected to an unusual degree of occasional pressure or friction, as in the palms of the hands of persons employed in rough manual labour; by the enlargement and increased hardness of muscles that are largely exercised; and by many other facts of a like kind. The increased power of nutrition put forth in such growth is greater than might be supposed; for the immediate effect of increased exercise of a part must be a greater using of its tissue, and might be expected to entail a permanent thinning or diminution of the substance of the part. But the energy with which fresh particles are formed is sufficient not only to replace completely those that are worn away, but to cause an increase in the substance of the part—the amount of this increase being proportioned to the more than usual degree in which its functions are exercised.

The growth of a part from undue exercise of its functions is always, in itself, a healthy process; and the increased size which results from it must be distinguished from the various kinds of enlargement to which the same part may be subject from disease. In the former case, the enlargement is due to an increased quantity of healthy tissue, providing more than the previous power to meet a particular emergency; the other may be the result of a deposit of morbid material within the natural structure of the part, diminishing, instead of augmenting, its fitness for its office. Such a healthy process of growth in a part, attended with increased power and activity of its functions, may, however, occur as the consequence of disease in some other part; in which case it is commonly called *Hypertrophy*, *i.e.*, excess of nutrition. The most familiar examples of this are in the increased thickness and robustness of the muscular walls of the cavities of the heart in cases of continued obstruction to the circulation; and in the increased development of the muscular coat of the urinary bladder when, from any cause, the free

discharge of urine from it is interfered with. In both these cases, though the origin of the growth is the consequence of disease, yet the growth itself is natural, and its end is the benefit of the economy; it is only common growth renewed or exercised in a part which had attained its size in due proportion to the rest of the body.

It may be further mentioned, in relation to the physiology of this subject, that when the increase of function, which is requisite in the cases from which hypertrophy results, cannot be efficiently discharged by mere increase of the ordinary tissue of the part, the development of a new and higher kind of tissue is frequently combined with this growth. An example of this is furnished by the uterus, in the walls of which, when it becomes enlarged by pregnancy, or by the growth of fibrous tumours, organic muscular fibres, found in a very ill-developed condition in its quiescent state, are then enormously developed, and provide for the expulsion of the fœtus or the foreign body. Other examples of the same kind are furnished by cases in which, from obstruction to the discharge of their contents and a consequently increased necessity for propulsive power, the coats of reservoirs and of ducts become the seat of development of organic muscular fibres, which could be said only just to exist in them before, or were present in a very imperfectly developed condition.

Respecting the mode and conditions of the process of growth, it need only be said, that its mode seems to differ only in degree from that of common maintenance of a part; more particles are removed from, and many more added to a growing tissue, than to one which only maintains itself. But so far as can be ascertained, the mode of removal, the disposition of the removed parts, and the insertion of the new particles, are as in simple maintenance.

The conditions also of growth are the same as those of common nutrition, and are equally or more necessary to its occurrence. When they are very favourable or in excess, growth may occur in the place of common nutrition. Thus hair may grow profusely in the neighbourhood of old ulcers, in consequence, apparently, of the excessive supply of blood to the

hair-bulbs and pulps; bones may increase in length when disease brings much blood to them; and cocks' spurs transplanted from their legs into their combs grow to an unnatural length; the conditions common to all these cases being both an increased supply of blood, and the capability, on the part of the growing tissue, of availing itself of the opportunity of increased absorption and nutrition thus afforded to it. In the absence of the last-named condition, increased supply of blood will not lead to increased nutrition.

CHAPTER XIII.

SECRETION.

Secretion is the process by which materials are separated from the blood, and from the organs in which they are formed, for the purpose either of serving some ulterior office in the economy, or being discharged from the body as excrement. In the former case, the separated materials are termed *secretions;* in the latter, they are named *excretions.*

Most of the secretions consist of substances which, probably, do not pre-exist in the same form in the blood, but require special organs and a process of elaboration for their formation, *e.g.*, the liver for the formation of bile, the mammary gland for the formation of milk. The excretions, on the other hand, commonly or chiefly consist of substances which, as urea, carbonic acid, and probably uric acid, exist ready-formed in the blood, and are merely abstracted therefrom. If from any cause, such as extensive disease or extirpation of an excretory organ, the separation of an excretion is prevented, and an accumulation of it in the blood ensues, it frequently escapes through other organs, and may be detected in various fluids of the body. But this is never the case with secretions; at least with those that are most elaborated; for after the removal of the special organs by which any of them is elaborated, it is no longer formed. Cases sometimes occur in which the secretion continues to be

formed by the natural organ, but not being able to escape towards the exterior, on account of some obstruction, is re-absorbed into the blood, and afterwards discharged from it by exudation in other ways; but these are not instances of true vicarious secretion, and must not be thus regarded.

These circumstances, and their final destination, are, however, the only particulars in which secretions and excretions can be distinguished; for, in general, the structure of the parts engaged in eliminating excretions, *e.g.*, the kidneys, is as complex as that of the parts concerned in the formation of secretions. And since the differences of the two processes of separation, corresponding with those in the several purposes and destinations of the fluids, are not yet ascertained, it will be sufficient to speak in general terms of the process of separation or secretion.

Every secreting apparatus possesses, as essential parts of its structure, a simple and apparently textureless membrane, named the *primary* or *basement-membrane;* certain *cells;* and *blood-vessels.* These three structural elements are arranged together in various ways; but all the varieties may be classed under one or other of two principal divisions, namely, *membranes* and *glands.*

SECRETING MEMBRANES.

The principal secreting membranes are the serous and synovial membranes, the mucous membranes, and the skin.*

Fig. 186.†

The serous membranes are especially distinguished by the characters of the endothelium covering their free surface: it

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* The skin will be described in a subsequent chapter.

† Fig. 186. Plan of a secreting membrane: *a*, *membrana propria*, or basement membrane; *b*, epithelium composed of secreting nucleated cells; *c*, layer of capillary blood-vessels (Sharpey).

always consists of a single layer of polygonal cells, the general characters of which have been already described (pp. 61, 62). The ground substance of most serous membranes consists of connective-tissue corpuscles of various forms lying in the branching spaces which constitute the "lymph canalicular system," and interwoven with bundles of white fibrous tissue, and numerous delicate elastic fibrillæ, together with blood-vessels, nerves and lymphatics.

In relation to the process of secretion, the layer of fibro-cellular tissue serves as a ground-work for the ramification of blood-vessels, lymphatics, and nerves. But in its usual form it is absent in some instances, as in the arachnoid covering the dura mater, and in the interior of the ventricles of the brain. The primary membrane and epithelium are probably always present, and are concerned in the formation of the fluid by which the free surface of the membrane is moistened.

The serous membranes are of two principal kinds: *1st.* Those which line visceral cavities,—the arachnoid, pericardium, pleuræ, peritoneum, and tunicæ vaginales. *2nd.* The synovial membranes lining the joints, and the sheaths of tendons and ligaments, with which, also, are usually included the synovial bursæ, or *bursæ mucosæ*, whether these be subcutaneous, or situated beneath tendons that glide over bones.

The serous membranes form closed sacs, and exist wherever the free surfaces of viscera come into contact with each other or lie in cavities unattached to surrounding parts. The viscera invested by a serous membrane are, as it were, pressed into the shut sac which it forms, carrying before them a portion of the membrane, which serves as their investment. To the law that serous membranes form shut sacs, there is, in the human subject, one exception, viz.: the opening of the Fallopian tubes into the abdominal cavity,—an arrangement which exists in man and all Vertebrata, with the exception of a few fishes.

The principal purpose of the serous and synovial membranes is to furnish a smooth, moist surface, to facilitate the movements of the invested organ, and to prevent the injurious effects of friction. This purpose is especially manifested in joints, in

which free and extensive movements take place; and in the stomach and intestines, which, from the varying quantity and movements of their contents, are in almost constant motion upon one another and the walls of the abdomen.

The fluid secreted from the free surface of the serous membranes is, in health, rarely more than sufficient to ensure the maintenance of their moisture. The opposed surfaces of each serous sac are at every point in contact with each other, and leave no space in which fluid can collect. After death, a larger quantity of fluid is usually found in each serous sac; but this, if not the product of manifest disease, is probably such as has transuded after death, or in the last hours of life. An excess of such fluid in any of the serous sacs constitutes dropsy of the sac.

The fluid naturally secreted by the serous membranes appears to be identical, in general and chemical characters, with the serum of the blood, or with very dilute liquor sanguinis. It is of a pale yellow or straw-colour, slightly viscid, alkaline, and, on account of the presence of albumen, coagulable by heat. The presence of a minute quantity of fibrin, at least in the dropsical fluids effused into the serous cavities, is shown by their partial coagulation into a jelly-like mass, on the addition of certain animal substances, or on mixture with certain fluids, especially such as contain cells (p. 106 *et seq.*). This similarity of the serous fluid to the liquid part of blood, and to the fluid with which most animal tissues are moistened, renders it probable that it is, in great measure, separated by simple transudation through the walls of the blood-vessels. The probability is increased by the fact that, in jaundice, the fluid in the serous sacs is, equally with the serum of the blood, coloured with the bile. But there is reason for supposing that the fluid of the cerebral ventricles and of the arachnoid sac are exceptions to this rule; for they differ from the fluids of the other serous sacs not only in being pellucid, colourless, and of much less specific gravity, but in that they seldom receive the tinge of bile in the blood, and are not coloured by madder, or other similar substances introduced abundantly into the blood.

It is also probable that the formation of synovial fluid is a process of more genuine and elaborate secretion, by means of the epithelial cells on the surface of the membrane, and especially of those which are accumulated on the edges and processes of the synovial fringes; for, in its peculiar density, viscidity, and abundance of albumen, synovia differs alike from the serum of blood and from the fluid of any of the serous cavities.

Mucous Membranes.

The *mucous membranes* line all those passages by which internal parts communicate with the exterior, and by which either matters are eliminated from the body or foreign substances taken into it. They are soft and velvety, and extremely vascular. Their general structure resembles that of serous membranes. It consists of epithelium, basement membrane, and fibro-cellular or areolar tissue containing blood-vessels, lymphatics, and nerves. The structure of mucous membranes is less uniform, especially as regards their epithelium, than that of serous membranes; but the varieties of structure in different parts are described in connection with the organs in which mucous membranes are present, and need not be here noticed in detail. The external surfaces of mucous membranes are attached to various other tissues; in the tongue, for example, to muscle; on cartilaginous parts, to perichondrium; in the cells of the ethmoid bone, in the frontal and sphenoid sinuses, as well as in the tympanum, to periosteum; in the intestinal canal, it is connected with a firm submucous membrane, which on its exterior gives attachment to the fibres of the muscular coat.

The mucous membranes are described as lining certain principal tracts—Gastro-Pulmonary and Genito-Urinary; the former being subdivided into the Digestive and Respiratory tracts. 1. The *Digestive tract* commences in the cavity of the mouth, from which prolongations pass into the ducts of the salivary glands. From the mouth it passes through the fauces, pharynx, and œsophagus, to the stomach, and is thence continued along the whole tract of the intestinal canal to the termination of the rectum, being in its course arranged in the various folds

and depressions already described, and prolonged into the ducts of the intestinal glands, the pancreas and liver, and into the gall-bladder. 2. The *Respiratory tract* includes the mucous membrane lining the cavity of the nose, and the various sinuses communicating with it, the lachrymal canal and sac, the conjunctiva of the eye and eyelids, and the prolongation which passes along the Eustachian tubes and lines the tympanum and the inner surface of the membrana tympani. Crossing the pharynx, and lining that part of it which is above the soft palate, the respiratory tract leads into the glottis, whence it is continued, through the larynx and trachea, to the bronchi and their divisions, which it lines as far as the branches of about $\frac{1}{50}$ of an inch in diameter, and continuous with it is a layer of delicate epithelial membrane which extends into the pulmonary cells. 3. The *Genito-urinary* tract, which lines the whole of the urinary passages, from their external orifice to the termination of the tubuli uriniferi of the kidneys, extends also into the organs of generation in both sexes, and into the ducts of the glands connected with them; and in the female becomes continuous with the serous membrane of the abdomen at the fimbriæ of the Fallopian tubes.

Along each of the above tracts, and in different portions of each of them, the mucous membrane presents certain structural peculiarities adapted to the functions which each part has to discharge; yet in some essential characters mucous membrane is the same, from whatever part it is obtained. In all the principal and larger parts of the several tracts, it presents, as just remarked, an external layer of epithelium, situated upon *basement-membrane*, and beneath this, a stratum of vascular tissue of variable thickness, which in different cases presents either outgrowths in the form of papillæ and villi, or depressions or involutions in the form of glands. But in the prolongations of the tracts, where they pass into gland-ducts, these constituents are reduced in the finest branches of the ducts to the epithelium, the primary or basement-membrane, and the capillary blood-vessels spread over the outer surface of the latter in a single layer.

The primary or basement-membrane is a thin transparent

layer, simple, homogeneous, and with no discernible structure, which on the larger mucous membranes that have a layer of vascular fibro-cellular tissue, may appear to be only the blastema or formative substance, out of which successive layers of epithelium-cells are formed. But in the minuter divisions of the mucous membranes, and in the ducts of glands, it is the layer continuous and correspondent with this basement-membrane that forms the proper walls of the tubes. The cells also which, lining the larger and coarser mucous membranes, constitute their epithelium, are continuous with, and often similar to those which, lining the gland-ducts, are called *gland-cells*. Indeed, no certain distinction can be drawn between the epithelium-cells of mucous membranes and gland-cells. In reference to their position, as covering surfaces, they might all be called epithelium-cells, whether they lie on open mucous membranes, or in gland-ducts; and in reference to the process of secretion, they might all be called gland-cells, or at least secreting-cells, since they probably all fulfil a secretory office by separating certain definite materials from the blood and from the part on which they are seated. It is only an artificial distinction which makes them epithelial cells in one place, and gland-cells in another.

It thus appears, that the tissues essential to the production of a secretion are, in their simplest form, a simple membrane, having on one surface blood-vessels, and on the other a layer of cells, which may be called either epithelium-cells or gland-cells. Glands are provided also with lymphatic vessels and nerves. The distribution of the former is not peculiar, and need not be here considered. Nerve-fibres are distributed both to the blood-vessels of the gland and to its ducts; and, in some glands, it is said, to the secreting cells also (p. 286).

The structure of the elementary portions of a secreting apparatus, namely epithelium, simple membrane, and blood-vessels, having been already described in this and previous chapters, we may proceed to consider the manner in which they are arranged to form the varieties of *secreting glands*.

SECRETING GLANDS.

The secreting glands are the organs to which the function of *secretion* is more especially ascribed: for they appear to be occupied with it alone. They present, amid manifold diversities of form and composition, a general plan of structure, by which they are distinguished from all other textures of the body; especially, all contain, and appear constructed with particular regard to, the arrangement of the cells, which, as already expressed, both line their tubes or cavities as an epithelium, and elaborate, as secreting cells, the substances to be discharged from them.

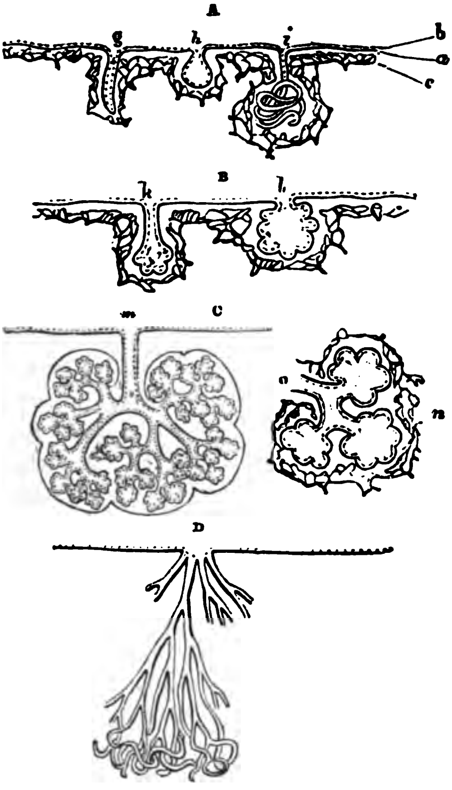
For convenience of description, they may be divided into three principal groups, the characters of each of which are determined by the different modes in which the sacculi or tubes containing the secreting cells are grouped:—

1. The *simple tubule*, or *tubular gland* (A, fig. 187), examples of which are furnished by the several tubular follicles in mucous membranes, especially by the follicles of Lieberkühn in the mucous membrane of the intestinal canal (p. 325), and the tubular glands of the stomach (p. 298). These appear to be simple tubular depressions of the mucous membrane on which they open, each consisting of an elongated gland vesicle, the wall of which is formed of primary membrane, and is lined with secreting cells arranged as an epithelium. To the same class may be referred the elongated and tortuous sudoriparous glands (p. 436), and the Meibomian follicles beneath the palpebral conjunctiva; though the latter are made more complex by the presence of small pouches along their sides (B, fig. 187), and form a connecting link between the members of this division and the next.

The *convoluted tubular glands* (D, fig. 187), such as the kidney and testis, form another division. These consist of tubules of membrane, lined with secreting cells arranged like an epithelium. Through nearly the whole of their long course, the tubules present an almost uniform size and structure; ultimately they terminate either in a cul-de-sac, or by dilating, as in the Malpighian capsules of the kidney, or by forming a simple loop and returning, as in the testicle.

2. The *aggregated glands*, including those formerly termed *conglomerate*, in which a number of vesicles or *acini* are arranged in groups or lobules (c, fig. 187). Such are all those

Fig. 187.*

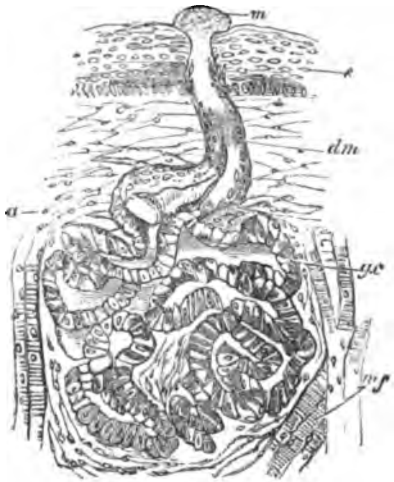


commonly called mucous glands (fig. 188) as those of the trachea and œsophagus, and the minute salivary glands. Such, also,

* Fig. 187. Plans of extension of secreting membrane by inversion or recession in form of cavities. A, simple glands, viz., *g*, straight tube; *h*, sac; *i*, coiled tube. B, multilocular crypts; *k*, of tubular form; *l*, saccular. C, racemose, or saccular compound gland; *m*, entire gland, showing branched duct and lobular structure; *n*, a lobule, detached with *o*, branch of duct proceeding from it. D, compound tubular gland (Sharpey).

are the lachrymal, the large salivary and mammary glands, Brunn's, Cowper's, and Duverney's glands, the pancreas and prostate. These various organs differ from each other only in secondary points of structure; such as, chiefly, the arrangement of their excretory ducts, the grouping of the *acini* and lobules, their connection by fibro-cellular tissue, and supply of blood-vessels. The acini commonly appear to be formed by a kind of fusion of the walls of several vesicles, which thus combine to form one cavity lined or filled with secreting cells which also occupy recesses from the main cavity. The smallest branches of the gland-ducts sometimes open into the centres of these cavities; sometimes the acini are clustered round the extremities, or by the sides of the ducts: but, whatever secondary arrangement there may be, all have the same essential character of rounded groups of vesicles containing gland-cells, and opening, either occasionally or permanently, by a common central cavity into minute ducts, which ducts in the large glands converge and unite to form larger and larger branches, and at length, by one common trunk, open on a free surface of membrane.

Fig. 188.*



Among these varieties of structure, all the permanent glands are alike in some essential points, besides those which they have in common with all truly secreting structures. They agree in

* Fig. 188. Mucous gland, from tongue of dog. *e*, epithelium, showing different shapes of nuclei at various depths; *m*, mucus discharged from orifice of *d m*, duct of mucous gland lined by epithelium, and containing a mass of mucus; *a*, areolar tissue of submucous layer; *m f*, muscular fibres of tongue; *g c*, gland cells of the various contorted tubes and acini of which the gland consists (Schofield).

presenting a large extent of secreting surface within a comparatively small space; in the circumstance that while one end of the gland-duct opens on a free surface, the opposite end is always closed, having no direct communication with blood-vessels, or any other canal; and in an uniform arrangement of capillary blood-vessels, ramifying and forming a network around the walls and in the interstices of the ducts and acini.

PROCESS OF SECRETION.

In secretion two distinct processes are concerned which may be spoken of as *physical* and *chemical.*

1. *Physical processes.*—These are such as can be closely imitated in the laboratory, inasmuch as they consist in the operation of well-known physical laws: they are—

(*a*) Filtration. (*b*) Diffusion.

(*a*) *Filtration* is simply the passage of a fluid through a porous membrane under the influence of pressure. If two fluids be separated by a porous membrane, and the pressure on one side is greater than on the other, it is evident that in the absence of counteracting osmotic influences (see below) there will be a filtration through the membrane until the pressure on the two sides is equalized. Of course there may only be fluid on one side of the membrane, as in the ordinary process of filtering through blotting paper, and then the filtration will continue as long as the pressure (in this case the weight of the fluid) is sufficient to force it through the pores of the filter.

The necessary inequality of pressure may be obtained either by diminishing it on one side, as in the case of cupping, or increasing it on the other, as in the case of the increased blood-pressure and consequent increased flow of urine resulting from copious drinking.

By filtration, not merely water but various salts in solution may transude from the blood-vessels.

(*b*) *Diffusion* is the passage of fluids through a moist animal membrane independent of pressure, and sometimes actually in opposition to it. (For a full account of the process see Chapter on Absorption.)

There must always be in this process two fluids differing in composition, one or both possessing an affinity for the intervening membrane, and the fluids capable of being mixed one with the other; the osmotic current continuing in each direction (when both fluids have an affinity for the membrane) until the chemical composition of the fluid on each side of the septum becomes the same.

It seems probable that some fluids, such as the secretions of serous membranes, are simply exudations or oozings (filtration) from the blood-vessels, whose qualities are determined by those of the liquor sanguinis, while the quantities are liable to variation, and are chiefly dependent upon the blood-pressure.

2. *Chemical processes.*—These constitute the process of *secretion* properly so-called as distinguished from mere transudation spoken of above. Such processes might more correctly be termed vital, inasmuch as they are intimately connected with the life and growth of the gland-cells, which, as they develop and grow, form in their interior the proper materials of the secretion and then discharge them (p. 288).

Thus, in the purely *physical* process of *transudation*, there is simply an oozing out of materials which pre-exist in the blood, and are merely separated from it; while in the *chemical* process of *secretion* various materials which do not exist as such in the blood are elaborated by the agency of the gland-cells from the blood, or, to speak more accurately, from the *plasma* which exudes from the blood-vessels into the interstices of the gland-textures.

The best evidence for this view is: *1st.* That cells and nuclei are constituents of all glands, however diverse their outer forms and other characters, and are in all glands placed on the surface or in the cavity whence the secretion is poured. *2nd.* That many secretions which are visible with the microscope may be seen in the cells of their glands before they are discharged. Thus, bile may be often discerned by its yellow tinge in the gland-cells of the liver; spermatozoids in the cells of the tubules of the testicles; granules of uric acid in those of the kidneys (of fish); fatty particles, like those of milk, in the cells of the mammary gland.

The process of secretion might, therefore, be said to be accomplished in, and by the life of, these gland-cells. They appear, like

the cells or other elements of any other organ, to develop, grow, and attain their individual perfection by appropriating nutriment from the adjacent blood-vessels and elaborating it, so that it shall form part of their own substance. In this perfected state, the cells subsist for some brief time, and when that period is over they appear to dissolve, wholly or in part, and yield their contents to the peculiar material of the secretion. And this appears to be the case in every part of the gland that contains the appropriate gland-cells; therefore not in the extremities of the ducts or in the acini alone, but in great part of their length.

In these things there is the closest resemblance between secretion and nutrition; for, if the purpose which the secreting glands are to serve in the economy be disregarded, their formation might be considered as only the process of nutrition of organs, whose size and other conditions are maintained in, and by means of, the continual succession of cells developing themselves and passing away. In other words, glands are maintained by the development of the cells, and their continuance in the perfect state: and the secretions are discharged as the constituent gland-cells degenerate and are set free. The processes of nutrition and secretion are similar, also, in their obscurity: there is the same difficulty in saying why, out of apparently the same materials, the cells of one gland elaborate the components of bile, while those of another form the components of milk, and of a third those of saliva, as there is in determining why one tissue forms cartilage, another bone, a third muscle, or any other tissue. In nutrition, also, as in secretion, some elements of tissues, such as the gelatinous tissues, are different in their chemical properties from any of the constituents ready-formed in the blood.

The *Discharge of Secretions* from glands may take place as soon as they are formed; or the secretion may be long retained within the gland or its ducts. The secretions of glands which are continually in active function for the purification of the blood, such as the kidneys, are generally discharged from the gland as rapidly as they are formed. But the secretions of those whose activity of function is only occasional are usually retained in the

ducts during the periods of the gland's inaction. And there are glands which are like both these classes, such as the lachrymal, which constantly secrete small portions of fluid, and on occasions of greater excitement discharge it more abundantly.

When discharged into the ducts, the further course of secretions is affected partly by the pressure from behind; the fresh quantities of secretion propelling those that were formed before. In the larger ducts, its propulsion is assisted by the contraction of their walls. All the larger ducts, such as the ureter and common bile-duct, possess in their coats plain muscular fibres; they contract when irritated, and sometimes manifest peristaltic movements. Bernard and Brown-Séquard, indeed, have observed rhythmic contractions in the pancreatic and bile-ducts, and also in the ureters and vasa deferentia. It is probable that the contractile power extends along the ducts to a considerable distance within the substance of the glands whose secretions can be rapidly expelled. Saliva and milk, for instance, are sometimes ejected with much force; doubtless by the energetic and simultaneous contraction of many of the ducts of their respective glands. The contraction of the ducts can only expel the fluid they contain through their main trunk; for at their opposite ends all the ducts are closed.

Circumstances influencing Secretion.—The influence of external conditions on the functions of glands, is manifested chiefly in alterations of the quantity of secretion; and among the principal of these conditions are variations in the quantity of blood, in the quantity of the peculiar materials for any secretion that it may contain, and in the conditions of the nerves of the glands.

An increase in the quantity of blood traversing a gland, coincides with an augmentation of its secretion. Thus, the mucous membrane of the stomach becomes florid when, on the introduction of food, its glands begin to secrete; the mammary gland becomes much more vascular during lactation; and all circumstances which give rise to an increase in the quantity of material secreted by an organ, produce, coincidently, an increased supply of blood.

Glands also secrete with increased activity when the blood contains more than usual of the materials they are designed to separate. Thus, when an excess of urea is in the blood, whether from excessive exercise, or from destruction of one kidney, a healthy kidney will excrete more than it did before. In the latter case, it will, at the same time, grow larger: an interesting fact, as proving both that secretion and nutrition in glands are identical, and that the presence of certain materials in the blood may lead to the formation of structures in which they may be incorporated.

Influence of the Nervous System on Secretion.

The process of secretion is largely influenced by the condition of the nervous system.

The exact mode in which the nervous system influences secretion must still be regarded as somewhat obscure. In part, it exerts its influence by increasing or diminishing the quantity of blood supplied to the secreting gland, in virtue of the power which it exercises over the contractility of the smaller blood-vessels; while it also has a more direct influence analogous to the *trophic* influence referred to in the chapter on NUTRITION. Its influence over secretion, as well as over other functions of the body, may be excited by causes acting directly upon the nervous centres, upon the nerves going to the secreting organ, or upon the nerves of other parts. In the latter case, a reflex action is produced: thus the impression produced upon the nervous centres by the contact of food in the mouth, is reflected upon the nerves supplying the salivary glands, and produces, through these, a more abundant secretion of saliva (p. 288).

Through the nerves, various conditions of the brain also influence the secretions. Thus, the thought of food may be sufficient to excite an abundant flow of saliva. And, probably, it is the mental state which excites the abundant secretion of urine in hysterical paroxysms, as well as the perspirations and, occasionally, diarrhœa, which ensue under the influence of terror, and the tears excited by sorrow or excess of joy. The quality of a secretion may also be affected by the mind; as in the cases in

which, through grief or passion, the secretion of milk is altered, and is sometimes so changed as to produce irritation in the alimentary canal of the child, or even death (Carpenter).

The secretions of some of the glands seem to bear a certain relation or antagonism to each other, by which an increased activity of one is usually followed by diminished activity of one or more of the others; and a deranged condition of one is apt to entail a disordered state in the others. Such relations appear to exist among the various mucous membranes: and the close relation between the secretion of the kidney and that of the skin is a subject of constant observation.

(For an account of direct experimental evidence of the influence of the nervous system on the process of secretion, see p. 288.)

CHAPTER XIV.

THE VASCULAR GLANDS; OR GLANDS WITHOUT DUCTS.

The materials separated from the blood by the ordinary process of secretion in glands, are always discharged from the organ in which they are formed, and either straightway expelled from the body, or if they are again received into the blood, it is only after they have been altered from their original condition, as in the cases of the saliva and bile. There appears, however, to be a modification of the process of secretion, in which certain materials are abstracted from the blood, undergo some change, and are added to the lymph or restored to the blood, without being previously discharged from the secreting organ, or made use of for any secondary purpose. The bodies in which this modified form of secretion takes place, are usually described as vascular glands, or glands without ducts, and include the spleen, the thymus and thyroid glands, the supra-renal capsules, and, according to Œsterlin and Ecker and Gull, the pineal gland and pituitary body; possibly, also the tonsils.

The solitary and agminate glands (Peyer's) of the intestine (p. 326), and lymph-glands in general, also closely resemble them;

indeed, both in structure and function, the vascular glands bear a close relation, on the one hand, to the true secreting glands, and on the other, to the lymphatic glands.

The evidence in favour of the view that these organs exercise a function analogous to that of secreting glands, has been chiefly obtained from investigations into their structure, which have shown that most of the glands without ducts contain the same essential structures as the secreting glands, except the ducts. They are mainly composed of vesicles, or sacculi, either simple and closed, as in the thyroid (fig. 189), and supra-renal capsules, or variously branched, and with the cavities of the several branches communicating in and by common canals, as in the thymus (fig. 190). These vesicles, like the acini of secreting

Fig. 189.*

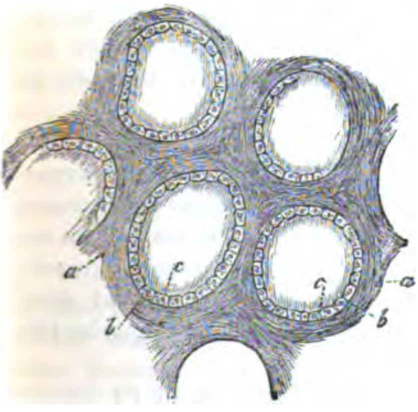
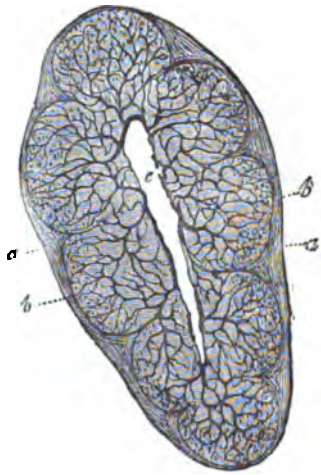


Fig. 190.†



* Fig. 189. Vesicles from the Thyroid Gland of a Child (from Kölliker) × 250. *a*, connective tissue between the vesicles; *b*, capsule of the vesicles; *c*, their epithelial lining.

† Fig. 190. Transverse Section of a Lobule of an injected infantile Thymus Gland (Kölliker) × 30. *a*, capsule of connective tissue surrounding the lobule; *b*, membrane of the glandular vesicles; *c*, cavity of the lobule, from which the larger blood-vessels are seen to extend towards and ramify in the spheroidal masses of the lobule.

glands, are formed of a delicate homogeneous membrane, are surrounded with and often traversed by a vascular plexus, and are filled with finely molecular albuminous fluid, suspended in which are either granules of fat, or cytoblasts or nuclei, or nucleated cells, or a mixture of all these.

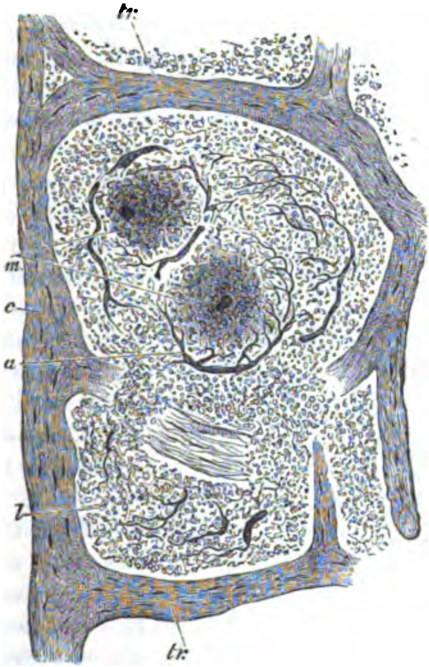
Structure of the Spleen.—The spleen is covered externally almost completely by a serous coat derived from the peritoneum, while within this is the proper fibrous coat or capsule of the organ. The latter, composed of connective tissue, with a large preponderance of elastic fibres, and a certain proportion of non-striated muscular tissue, forms the immediate investment of the spleen. Prolonged from its inner surface are fibrous processes or *trabeculæ,* which enter the interior of the organ, and, dividing and anastomosing in all parts, form a kind of supporting framework or *stroma,* in the interstices of which the proper substance of the spleen (*spleen-pulp*) is contained (fig. 191). At the *hilus* of the spleen, or the part at which the blood-vessels, nerves, and lymphatics enter, the fibrous coat is prolonged into the spleen-substance in the form of investing sheaths for the arteries and veins, which sheaths again are connected with the *trabeculæ* before referred to.

The *spleen-pulp,* which is a dark red or reddish-brown colour, is composed chiefly of cells. Of these, some are granular corpuscles resembling the lymph-corpuscles, both in general appearance and in being able to perform amœboid movements; others are red blood-corpuscles of normal appearance or variously changed; while there are also large cells containing either pigment allied to the colouring matter of the blood, or rounded corpuscles like red blood-cells.

The splenic artery which enters the spleen by its concave surface or *hilus* divides and subdivides, with but little anastomosis between its branches, in the midst of the spleen-pulp, at the same time that its branches are sheathed, as before said, by the fibrous coat, which they, so to speak, carry into the spleen with them. Ending in capillaries, they either communicate, as in other parts of the body, with the radicles of the veins, or end in lacunar spaces in the spleen-pulp, from which veins arise (Gray).

The walls of the smaller veins are more or less incomplete, and readily allow lymphoid corpuscles to be swept into the blood-current.

Fig. 191.*



"The blood traverses the network of the pulp, and interstices of the lymphoid cells contained in the latter, in the same manner as the water of a river finds its way among the pebbles of its bed: the blood from the arterial capillaries is emptied into a system of intermediate passages, which are directly bounded by the cells and fibres of the network of the pulp, and from which

* Fig. 191. Section of Dog's Spleen Injected: *c*, capsule, consisting of dense fibrous tissue with scattered nuclei; *tr*, trabeculæ of similar structure; *m*, two Malpighian bodies with numerous small arteries and capillaries; *a*, artery; *l*, lymphoid tissue, consisting of closely packed lymphoid cells supported by very delicate retiform tissue: a light space unoccupied by cells is seen all round the trabeculæ, which corresponds to the "lymph path" in lymphatic glands (Schofield).

the smallest venous radicles with their cribriform walls take origin" (Frey).

The veins are large and very distensible: the whole tissue of the spleen is highly vascular, and becomes readily engorged with blood: the amount of distension is, however, limited by the fibrous and muscular tissue of its capsule and trabeculæ, which forms an investment and support for the pulpy mass within.

On the face of a section of the spleen can be usually seen, readily with the naked eye, minute, scattered, rounded or oval whitish spots, mostly from $\frac{1}{30}$ to $\frac{1}{60}$ inch in diameter. These are the *Malpighian corpuscles* of the spleen, and are situated on the sheaths of the minute splenic arteries, of which, indeed, they may be said to be outgrowths (fig. 192). For while the sheaths of the larger arteries are constructed of ordinary connective tissue, this has become modified where it forms an investment for the smaller vessels, so as to be a fine retiform tissue, with abundance of corpuscles, like lymph-corpuscles, contained in its meshes, and the Malpighian corpuscles are but small outgrowths of this *cytogenous* or cell-bearing connective tissue. They are composed of masses of corpuscles, intersected in all parts by a delicate fibrillar tissue, which, though it invests the Malpighian bodies, does not form a complete capsule. Blood-capillaries traverse the Malpighian corpuscles and form a plexus in their interior. The structure of a

Fig. 192.*

* Fig. 192. The figure shows a portion of a small artery, to one of the twigs of which the Malpighian corpuscles are attached.

Malpighian corpuscle of the spleen is, therefore, very similar to that of lymphatic-gland substance (p. 379).

The opinion that the vascular glands thus serve for the higher organization of the blood, is supported by their being all especially active in the discharge of their functions during fœtal life and childhood, when, for the development and growth of the body, the most abundant supply of highly organized blood is necessary. The bulk of the thymus gland, in proportion to that of the body, appears to bear almost a direct proportion to the activity of the body's development and growth, and when, at the period of puberty, the development of the body may be said to be complete, the gland wastes, and finally disappears. The thyroid gland and supra-renal capsules, also, though they probably never cease to discharge some amount of function, yet are proportionally much smaller in childhood than in fœtal life and infancy; and with the year's advancing to the adult period, they diminish yet more in proportionate size and apparent activity of function. The spleen more nearly retains its proportionate size, and enlarges nearly as the whole body does.

The function of the vascular glands seems not essential to life, at least not in the adult. The thymus wastes and disappears; no signs of illness attend some of the diseases which wholly destroy the structure of the thyroid gland; and the spleen has been often removed in animals, and in a few instances in men, without any evident ill-consequence. It is possible that, in such cases, some compensation for the loss of one of the organs may be afforded by an increased activity of function in those that remain.

Although the functions of all the vascular glands may be similar, in so far as they may all alike serve for the elaboration and maintenance of the blood, yet each of them probably discharges a peculiar office, in relation either to the whole economy, or to that of some other organ. Respecting the special office of the thyroid gland, nothing reasonable can be suggested; nor is there any certain evidence concerning that of the supra-renal capsules.

Mr. J. Hutchinson, and, more recently, Dr. Wilks, Dr. Greenhow, and others, following out Dr. Addison's discovery, have, by the collection of large

numbers of cases in which the supra-renal capsules were diseased, demonstrated most satisfactorily the very close relation subsisting between disease of these organs and brown discoloration of the skin (Addison's disease); but the explanation of this relation is still involved in obscurity, and consequently does not aid much in determining the functions of the supra-renal capsules.

Respecting the thymus gland, the observations of Mr. Simon, confirmed by those of Friedleben and others, have shown that in the hybernating animals, in which it exists throughout life, as each successive period of hybernation approaches, the thymus greatly enlarges and becomes laden with fat, which accumulates in it and in fat-glands connected with it, in even larger proportions than it does in the ordinary seats of adipose tissue. Hence it appears to serve for the storing up of materials which, being re-absorbed in inactivity of the hybernating period, may maintain the respiration and the temperature of the body in the reduced state to which they fall during that time.

With respect to the office of the spleen, we have somewhat more definite information. (1.) The large size which it gradually acquires towards the termination of the digestive process, and the great increase observed about this period in the amount of the finely-granular albuminous plasma within its parenchyma, and the subsequent gradual decrease of this material, seem to indicate that this organ is concerned in elaborating the albuminous materials of food, and for a time storing them up, to be gradually introduced into the blood, according to the demands of the general system.

(2.) It seems not improbable that, as Hewson originally suggested, the spleen, and perhaps to some extent the other vascular glands, are, like the lymphatic glands, engaged in the formation of the germs of subsequent blood-corpuscles. For it seems quite certain, that the blood of the splenic vein contains an unusually large amount of white corpuscles; and in the disease termed leucocythæmia, in which the pale corpuscles of the blood are remarkably increased in number, there is almost always found an hypertrophied state of the spleen or thyroid body, or some of the lymphatic glands. Accordingly, there seems to be a close analogy in function between the so-called

vascular and the lymphatic glands: the former elaborating albuminous principles, and forming the germs of new blood-corpuscles out of alimentary materials absorbed by the blood-vessels; the latter discharging the like office on nutritive materials taken up by the general absorbent system. In Kölliker's opinion, the development of colourless and also coloured corpuscles of the blood is one of the essential functions of the spleen, into the veins of which the new-formed corpuscles pass, and are thus conveyed into the general current of the circulation.

(3.) There is reason to believe, that in the spleen many of the red corpuscles of the blood, those probably which have discharged their office and are worn out, undergo disintegration; for in the coloured portion of the spleen-pulp an abundance of such corpuscles, in various stages of degeneration, are found, while the red corpuscles in the splenic venous blood are said to be relatively diminished. According to Kölliker's description of this process of disintegration, the blood-corpuscles, becoming smaller and darker, collect together in roundish heaps, which may remain in this condition, or become each surrounded by] a cell-wall. The cells thus produced may contain from one to twenty blood-corpuscles in their interior. These corpuscles become smaller and smaller; exchange their red for a golden yellow, brown, or black colour; and, at length, are converted into pigment-granules, which by degrees become paler and paler, until all colour is lost. The corpuscles undergo these changes whether the heaps of them are enveloped by a cell-wall or not.

(4.) Besides these, its supposed direct offices, the spleen is believed to fulfil some purpose in regard to the portal circulation, with which it is in close connection. From the readiness with which it admits of being distended, and from the fact that it is generally small while gastric digestion is going on, and enlarges when that act is concluded, it is supposed to act as a kind of vascular reservoir, or diverticulum to the portal system, or more particularly to the vessels of the stomach. That it may serve such a purpose is also made probable by the enlargement which it undergoes in certian affections of the heart and liver, attended with obstruction to the passage of blood through the latter

organ, and by its diminution when the congestion of the portal system is relieved by discharges from the bowels, or by the effusion of blood into the stomach. This mechanical influence on the circulation, however, can hardly be supposed to be more than a very subordinate part of the office of an organ of so great complexity as the spleen, and containing so many other structures besides blood-vessels. The same may also be said with regard to the opinion that the thyroid gland is important as a diverticulum for the cerebral circulation, or the thymus for the pulmonary in childhood. These, like the spleen, must have peculiar and higher, though as yet ill-understood, offices.

CHAPTER XV.

THE SKIN AND ITS SECRETION.

To complete the consideration of the processes of organic life, and especially of those which, by separating materials from the blood, maintain it in the state necessary for the nutrition of the body, the structure and functions of the skin must be now considered: for besides the purposes which it serves—(1), as an external integument for the protection of the deeper tissues, and (2), as a sensitive organ in the exercise of touch, it is also (3), an important excretory, and (4), an absorbing organ; while it plays a most important part in (5) the regulation of the temperature of the body.

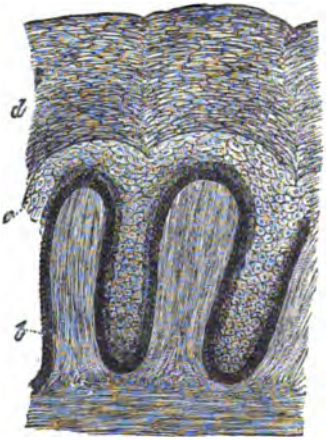
Structure of the Skin.

The skin consists, principally, of a layer of vascular tissue, named the *corium*, *derma*, or *cutis vera*, and an external covering of epithelium termed the *cuticle* or *epidermis*. Within and beneath the corium are imbedded several organs with special functions, namely *sudoriparous* glands, *sebaceous* glands, and *hair-follicles*; and on its surface are sensitive *papillæ*. The so-called appendages of the skin—the *hair* and *nails*—are modifications of the epidermis.

Epidermis.—The *epidermis* is composed of several layers of

squamous epithelial cells (p. 59), the deeper cells, however, being rounded or elongated, and in the latter instance having their long axis arranged vertically as regards the general surface of the skin, while the more superficial cells are flattened and scaly (fig. 193). The deeper part of the epidermis, which is softer and more opaque than the superficial, is called the *rete mucosum*. Many of the epidermal cells contain pigment, and the varying quantity of this is the source of the different shades of tint in the skin, both of individuals and races. The colouring matter is contained chiefly in the deeper cells composing the *rete mucosum*, and becomes less evident in them as they are gradually pushed up by those under them, and become, like their predecessors, flattened and scale-like (fig. 193). It is by this process of production from beneath, to make up for the waste at the surface, that the growth of the cuticle is effected.

Fig. 193.*



The thickness of the epidermis on different portions of the skin is directly proportioned to the friction, pressure, and other sources of injury to which it is exposed; and the more it is subjected to such injury, within certain limits, the more does it grow, and the thicker and more horny does it become; for it serves as well to protect the sensitive and vascular cutis from injury from without, as to limit the evaporation of fluid from the blood-vessels. The adaptation of the epidermis to the latter purposes may be well shown by exposing to the air two dead hands or feet, of which one has its epidermis perfect, and the other is deprived of it; in a day, the skin of the latter will be-

* Fig. 193. Skin of the negro, in a vertical section. *a*, *a*, cutaneous papillæ; *b*, undermost and dark coloured layer of oblong vertical epidermis-cells; *c*, mucous or Malpighian layer; *d*, horny layer × 250 (Sharpey).

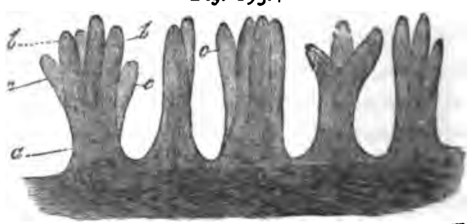
come brown, dry, and horn-like, while that of the former will almost retain its natural moisture.

Cutis vera.—The *corium* or *cutis*, which rests upon a layer of adipose and cellular tissue of varying thickness, is a dense and tough, but yielding and highly elastic structure, composed of fasciculi of fibro-cellular tissue, interwoven in all directions, and forming, by their interlacements, numerous spaces or areolæ. These areolæ are large in the deeper layers of the cutis, and are there usually filled with little masses of fat (fig. 196): but, in the superficial parts, they are small or entirely obliterated. Plain muscular fibre is also abundantly present (p. 584).

By means of its toughness, flexibility, and elasticity, the skin is eminently qualified to serve as the general integument of the body, for defending the internal parts from external violence, and readily yielding and adapting itself to their various movements and changes of position. But, from the abundant supply of sensitive nerve-fibres which it receives, it is enabled to fulfil a not less important purpose in serving as the principal organ of the sense of touch. The entire surface of the skin is extremely sensitive, but its tactile properties are due chiefly to the abundant papillæ with which it is studded. These papillæ are conical elevations of the corium, with a single or divided free extremity, more prominent and more densely set at some parts than at others (figs. 194 and 195). The parts on which they are most

Fig. 194.*

Fig. 195.†

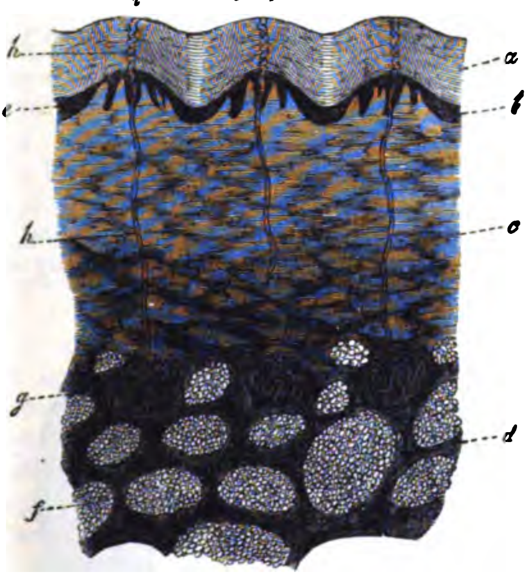


* Fig. 194. Papillæ, as seen with a microscope, on a portion of the true skin, from which the cuticle has been removed (Breschet).

† Fig. 195. Compound papillæ from the palm of the hand, magnified 60 diameters; *a*, basis of a papilla; *b*, *b*, divisions or branches of the same; *c*, *c*, branches belongiug to papillæ, of which the bases are hidden from view (Kölliker).

abundant and most prominent are the palmar surface of the hands and fingers, and the soles of the feet—parts, therefore, in which the sense of touch is most acute. On these parts they are disposed in double rows, in parallel curved lines, separated from each other by depressions (fig. 196). Thus they may be seen easily on the palm, whereon each raised line is composed of a double row of papillæ, and is intersected by short transverse

Fig. 196.*

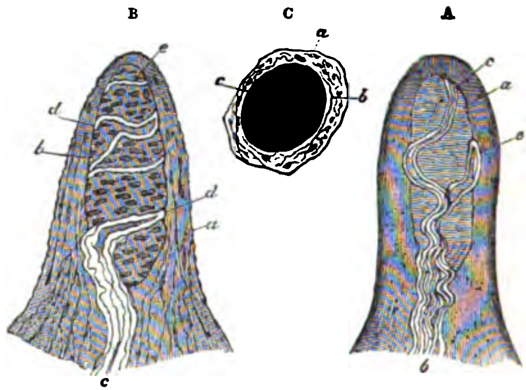


lines or furrows corresponding with the interspaces between the successive pairs of papillæ. Over other parts of the skin they are more or less thinly scattered, and are scarcely elevated above the surface. Their average length is about $\frac{1}{100}$th of an inch, and at their base they measure about $\frac{1}{250}$th of an in. in diameter. Each papilla is abundantly supplied with blood, receiving from the

* Fig. 196. Vertical section of the skin and subcutaneous tissue, from end of the thumb, across the ridges and furrows, magnified 20 diameters : *a*, horny, and *b*, mucous layer of the epidermis ; *c*, corium ; *d*, *panniculus adiposus ; e*, papillæ on the ridges ; *f*, fat cluster ; *g*, sweat-glands ; *h*, sweat-ducts ; *i*, their openings on the surface (Kölliker).

vascular plexus in the cutis one or more minute arterial twigs, which divide into capillary loops in its substance, and then reunite into a minute vein, which passes out at its base. The abundant supply of blood which the papillæ thus receive explains the turgescence or kind of erection which they undergo when the circulation through the skin is active. The majority, but not all, of the papillæ contain also one or more terminal nerve-fibres, from the ultimate ramifications of the cutaneous plexus, on which their exquisite sensibility depends. The exact mode in which these nerve-fibres terminate is not yet satisfactorily determined. In some parts, especially those in which the sense of touch is highly developed, as for example, the palm of the hand and the lips, the fibres appear to terminate, in many of the papillæ, by one or more free ends in the substance of a dilated oval-shaped body, not unlike a Pacinian corpuscle (figs. 225, 226), occupying the principal part of the interior of the papilla, and termed a *touch-corpuscle* (fig. 197). The nature of this body is obscure.

Fig. 197*.



* Fig. 197. Papillæ from the skin of the hand, freed from the cuticle and exhibiting tactile corpuscles. A. Simple papilla with four nerve-fibres: *a*, tactile corpuscle; *b*, nerves. B. Papilla treated with acetic acid: *a*, cortical layer with cells and fine elastic filaments; *b*, tactile corpuscle with transverse nuclei; *c*, entering nerve with neurilemma or perineurium; *d*, nerve-fibres winding round the corpuscle. C. Papilla viewed from above so as to appear as a cross section: *a*, cortical layer; *b*, nerve-fibre; *c*, sheath of the tactile corpuscle containing nuclei; *d*, core × 350 (Kölliker).

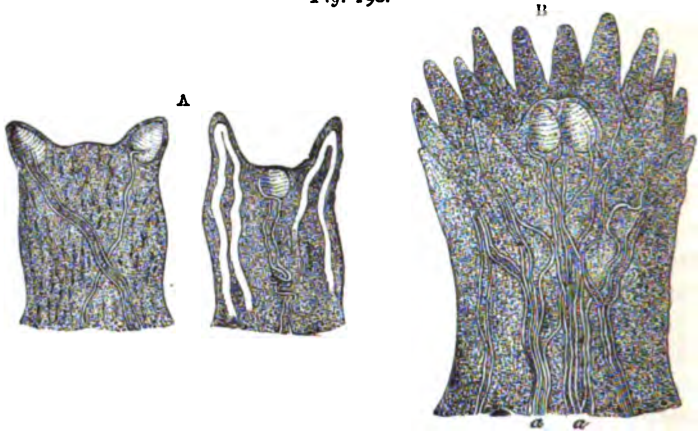
Kölliker, Huxley, and others, regard it as little else than a mass of fibrous or connective tissue, surrounded by elastic fibres, and formed, according to Huxley, by an increased development of the neurilemma of the nerve-fibres, entering the papillæ. Wagner, however, to whom seems to belong the merit of first fully describing these bodies, believes that, instead of thus consisting of a homogeneous mass of connective tissue, they are special and peculiar bodies of laminated structure, directly concerned in the sense of touch. They do not occur in all the papillæ of the parts where they are found, and, as a rule, in the papillæ in which they are present there are no blood-vessels. Since these peculiar bodies in which the nerve-fibres end are only met with in the papillæ of highly sensitive parts, it may be inferred that they are specially concerned in the sense of touch, yet their absence from the papillæ of other tactile parts shows that they are not essential to this sense.

Closely allied in structure to the Pacinian corpuscles and touch-corpuscles are some little bodies about $\frac{1}{600}$ of an inch in diameter, first particularly described by Krause, and named by him "end-bulbs." They are generally oval or spheroidal, and composed externally of a coat of connective tissue enclosing a softer matter, in which the extremity of a nerve terminates. These bodies have been found chiefly in the lips, tongue, palate, and the skin of the glans penis (fig. 198).

Although destined especially for the sense of touch, the papillæ are not so placed as to come into direct contact with external objects; but, like the rest of the surface of the skin, are covered by one or more layers of epithelium, forming the cuticle or epidermis. The papillæ adhere very intimately to the cuticle, which is thickest in the spaces between them, but tolerably level on its outer surface: hence, when stripped off from the cutis, as after maceration, its internal surface presents a series of pits and elevations corresponding to the papillæ and their interspaces, of which it thus forms a kind of mould. Besides affording by its impermeability a check to undue evaporation from the skin, and providing the sensitive cutis with a protecting investment, the cuticle is of service in relation

to the sense of touch. For by being thickest in the spaces, between the papillæ, and only thinly spread over the summits of these processes, it may serve to subdivide the sentient surface of the skin into a number of isolated points, each of which is

Fig. 198.*



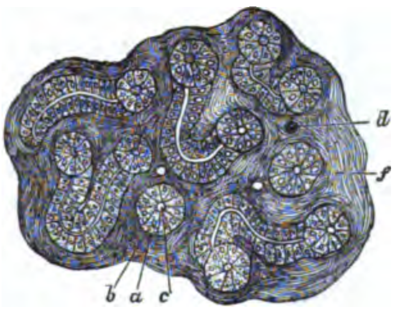
capable of receiving a distinct impression from an external body. By covering the papillæ it renders the sensation produced by external bodies more obtuse, and in this manner also is subservient to touch: for unless the very sensitive papillæ were thus defended, the contact of substances would give rise to pain, instead of the ordinary impressions of touch. This is shown in the extreme sensitiveness and loss of tactile power in a part of the skin when deprived of its epidermis. If the cuticle is very thick, however, as on the heel, touch becomes imperfect, or is lost, through the inability of the tactile papillæ to receive impressions through the dense and horny layer covering them.

Sudoriparous Glands.—In the middle of each of the transverse furrows between the papillæ, and irregularly scattered between the bases of the papillæ in those parts of the surface of the body

* Fig. 198. End-bulbs in papillæ (magnified) treated with acetic acid. A, from the lips; the white loops in one of them are capillaries. B, from the tongue. Two end-bulbs seen in the midst of the simple papillæ: *a*, *a*, nerves (Kölliker).

in which there are no furrows between them, are the orifices of ducts of the sudoriparous or sweat glands, by which a large portion of the aqueous and gaseous materials excreted by the skin are separated. Each of these glands consists of a small lobular mass, formed of a coil of tubular gland-duct, surrounded by blood-vessels and embedded in the subcutaneous adipose tissue (fig. 196). From this mass, the duct ascends, for a short distance, in a spiral manner through the deeper part of the cutis, then passing straight, and then sometimes again becoming spiral, it passes through the cuticle and opens by an oblique valve-like aperture. In the parts where the epidermis is thin, the ducts themselves are thinner and more nearly straight in their course (fig. 200). The duct, which maintains nearly the same diameter throughout, is lined with a layer of columnar epithelium (fig. 199) continuous with the epidermis; while the part which passes through the epidermis is composed of the latter structure only; the cells which immediately form the boundary of the canal in this part being somewhat differently arranged from those of the adjacent cuticle.

Fig. 199.*



The sudoriparous glands are abundantly distributed over the whole surface of the body; but are especially numerous, as well as very large, in the skin of the palm of the hand, where, according to Krause, they amount to 2736 in each superficial square inch, and according to Mr. Erasmus Wilson, to as many as 3528. They are almost equally abundant and large in the skin of the sole. The glands by which the peculiar odorous matter of the axillæ is secreted form a nearly complete layer under the cutis, and are like the ordinary sudoriparous glands, except in being larger and having very short ducts. In the neck and back, where they are least numerous, the glands

* Fig. 199. Glomeruli of sudoriparous gland, divided in various directions. *a*, sheath of the gland; *b*, columnar epithelial lining of gland tube; *c*, lumen of tube; *d*, divided blood-vessel; *f*, loose connective tissue, forming a capsule to the gland (Biesiadecki).

amount to 417 on the square inch (Krause). Their total number Krause estimates at 2,381,248; and, supposing the orifice of each gland to present a surface of $\frac{1}{56}$th of a line in diameter (and regarding a line as equal to $\frac{1}{10}$th of an inch), he reckons that the whole of the glands would present an evaporating surface of about eight square inches.

The peculiar bitter yellow substance secreted by the skin of the external auditory passage is named *cerumen*, and the glands themselves *ceruminous* glands; but they do not much differ in structure from the ordinary sudoriparous glands.

Sebaceous Glands.—Besides the perspiration, the skin secretes a peculiar fatty matter, and for this purpose is provided with another set of special organs, termed *sebaceous glands* (fig. 200), which, like the sudoriparous glands, are abundantly distributed over most parts of the body. They are most numerous in parts largely supplied with hair, as the scalp and face, and are thickly distributed about the entrances of the various passages into the body, as the anus, nose, lips, and external ear. They are entirely absent from the palmar surface of the hands and the plantar surfaces of the feet. They are minutely lobulated glands, composed of an aggregate of small vesicles or sacculi filled with opaque white substances, like soft ointment. Minute capillary vessels overspread them; and their ducts open either on the surface of the skin, close to a hair, or, which is more usual, directly into the follicle of the hair. In the latter case, there are generally two glands to each hair (fig. 200).

Fig. 200.*

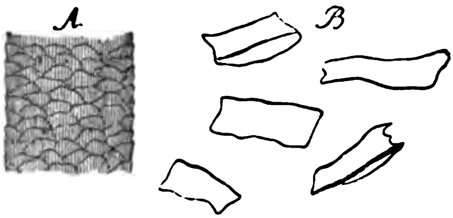
Structure of Hair and Nails.

Hair.—A hair is produced by a peculiar growth and modification of the epidermis. Externally it is covered by a layer of

* Fig. 200. Sebaceous and Sudoriparous glands of the skin:—1, the thin cuticle; 2, the cutis; 3, adipose tissue; 4, a hair, in its follicle (5); 6, sebaceous gland, opening into the follicle of the hair by an efferent duct; 7, sudoriparous gland (Gurlt).

fine scales closely imbricated, or overlapping like the tiles of a house, but with the free edges turned upwards (fig. 201, A). It is called the *cuticle* of the hair. Beneath this is a much thicker layer of elongated horny cells, closely packed together so as to resemble a fibrous structure. This, very commonly, in the human subject, occupies the whole of the inside of the hair;

Fig. 201.*



but in some cases there is left a small central space filled by a substance called the *medulla* or *pith*, composed of small collections of irregularly shaped cells, containing fat- and pigment-granules.

The follicle, in which the root of each hair is contained (fig. 202), forms a tubular depression from the surface of the skin,—descending into the subcutaneous fat, generally to a greater depth than the sudoriparous glands, and at its deepest part enlarging in a bulbous form, and often curving from its previous rectilinear course. It is lined throughout by cells of epithelium, continuous with those of the epidermis, and its walls are formed of pellucid membrane, which commonly, in the follicles of the largest hairs, has the structure of vascular fibro-cellular tissue. At the bottom of the follicle is a small papilla, or projection of true skin, and it is by the production and out-growth of epidermal cells from the surface of this papilla that the hair is formed. The inner wall of the follicle is lined by epidermal cells continuous with those covering the general surface of the skin; as if indeed the follicle had been formed by a simple

* Fig. 201. *A*, surface of a white hair, magnified 160 diameters. The wave lines mark the upper or free edges of the cortical scales. *B*, separated scales, magnified 350 diameters (Kölliker).

thrusting in of the surface of the integument (fig. 202). This epidermal lining of the hair-follicle, or *root-sheath* of the hair, is composed of two layers, the inner one of which is so moulded on the imbricated scaly cuticle of the hair, that its inner surface becomes imbricated also, but of course in the opposite direction. When a hair is pulled out, the inner layer of the *root-sheath* and part of the outer layer also are commonly pulled out with it.

Fig. 202.*

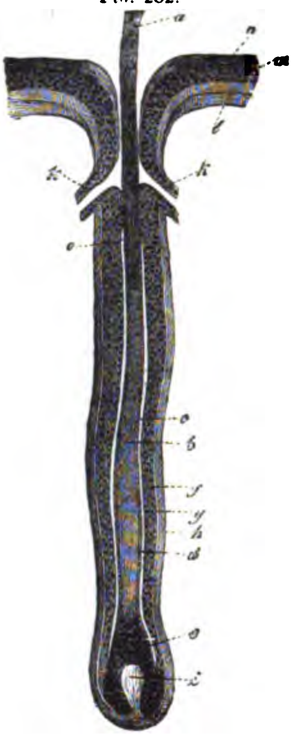


Fig. 203.†

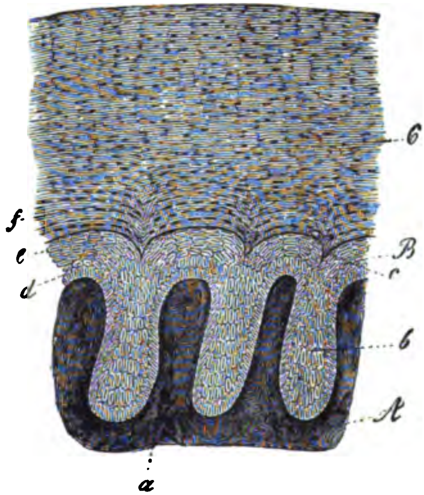
* Fig. 202. Medium-sized hair in its follicle, magnified 50 diameters. *a*, stem cut short; *b*, root; *c*, knob; *d*, hair cuticle; *e*, internal, and *f*, external root-sheath; *g*, *h*, dermic coat of follicle; *i*, papilla; *k*, *k*, ducts of sebaceous glands; *l*, corium; *m*, mucous layer of epidermis; *o*, upper limit of internal root-sheath (Kölliker). See also fig. 262.

† Fig. 203. Magnified view of the root of a hair (Kohlrausch). *a*, stem or shaft of hair cut across; *b*, inner, and *c*, outer layer of the epidermal lining of the hair-follicle, called also the inner and outer root-sheath; *d*, dermal or external coat of the hair-follicle, shown in part, *e*, imbricated scales about to form a cortical layer on the surface of the hair. The adjacent cuticle of the root-sheath is not represented, and the papilla is hidden in the lower part of the knob where that is represented lighter.

Nails.—A *nail*, like a hair, is a peculiar arrangement of epidermal cells, the undermost of which, like those of the general surface of the integument, are rounded or elongated, while the superficial are flattened, and of more horny consistence. That specially modified portion of the corium, or true skin, by which the nail is secreted, is called the *matrix*.

The back edge of the nail, or the *root* as it is termed, is received into a shallow crescentic groove in the *matrix*, while the front part is free, and projects beyond the extremity of the digit. The intermediate portion of the nail rests by its broad under surface on the front part of the matrix, which is here called the *bed* of the nail. This part of the matrix is not uniformly smooth on the surface, but is raised in the form of longitudinal and nearly parallel ridges or laminæ, on which are moulded the epidermal cells of which the nail is made up (fig. 204).

Fig. 204.*



The growth of the nail, like that of a hair, or of the epidermis generally, is effected by a constant production of cells from beneath and behind, to take the place of those which are worn or cut away. Inasmuch, however, as the posterior edge of the nail, from its being lodged in a groove of the skin, cannot grow backwards, on addi-

* Fig. 204. Vertical transverse section through a small portion of the nail and matrix largely magnified (Kölliker).

A, corium of the nail-bed, raised into ridges or laminæ *a*, fitting in between corresponding laminæ *b*, of the nail. *B*, Malpighian, and *C*, horny layer of nail : *d*, deepest and vertical cells ; *e*, upper flattened cells of Malpighian layer.

tions being made to it, so easily as it can pass in the opposite direction, any growth at its hinder part pushes the whole forwards. At the same time fresh cells are added to its under surface, and thus each portion of the nail becomes gradually thicker as it moves to the front, until, projecting beyond the surface of the matrix, it can receive no fresh addition from beneath, and is simply moved forwards by the growth at its root, to be at last worn away or cut off.

Excretion by the Skin.

The skin, as already stated, is the seat of a two-fold excretion; of that formed by the sebaceous glands and hair-follicles, and of the more watery fluid, the *sweat* or *perspiration*, eliminated by the sudoriparous glands.

The secretion of the *sebaceous* glands and *hair-follicles* (for their products cannot be separated) consists of cast-off epithelium-cells, with nuclei and granules, together with an oily matter, extractive matter, and stearin; in certain parts, also, it is mixed with a peculiar odorous principle, which is said by Dr. Fischer to contain caproic, butyric, and rutic acids. It is, perhaps, nearly similar in composition to the unctuous coating, or *vernix caseosa*, which is formed on the body of the fœtus while in the uterus, and which contains large quantities of ordinary fat (J. Davy). Its purpose seems to be that of keeping the skin moist and supple, and, by its oily nature, of both hindering the evaporation from the surface, and guarding the skin from the effects of the long-continued action of moisture. But while it thus serves local purposes, its removal from the body entitles it to be reckoned among the excretions of the skin; though the share it has in the purifying of the blood cannot be discerned.

The fluid secreted by the *sudoriparous* glands is usually formed so gradually, that the watery portion of it escapes by evaporation as fast as it reaches the surface. But, during strong exercise, exposure to great external warmth, in some diseases, and when evaporation is prevented, the secretion becomes more sensible, and collects on the skin in the form of drops of fluid. A good analysis of the secretion of these glands, unmixed with

other fluids secreted from the skin, can scarcely be made; for the quantity that can be collected pure is very small. Krause, in a few drops from the palm of the hand, found an acid reaction and an oily matter, with water.

The *perspiration* of the skin, as the term is sometimes employed in physiology, includes all that portion of the secretions and exudations from the skin which passes off by evaporation; the *sweat* includes that which may be collected only in drops of fluid on the surface of the skin. The two terms are, however, most often used synonymously; and for distinction, the former is called *insensible* perspiration: the latter *sensible* perspiration. The fluids are the same, except that the sweat is commonly mingled with various substances lying on the surface of the skin. The contents of the sweat are, in part, matters capable of assuming the form of vapour, such as carbonic acid and water, and in part, other matters which are deposited on the skin, and mixed with the sebacous secretion.

Thenard collected the perspiration in a flannel shirt which had been washed in distilled water, and found in it chloride of sodium, acetic acid, some phosphate of sodium, traces of phosphate of calcium, and oxide of iron, together with an animal substance. In sweat which had run from the forehead in drops, Berzelius found lactic acid, chloride of sodium, and chloride of ammonium. Anselmino placed his arm in a glass cylinder, and closed the opening around it with oiled silk, taking care that the arm touched the glass at no point. The cutaneous exhalation collected on the interior of the glass, and ran down as a fluid: on analysing this, he found water, acetate of ammonia, and carbonic acid; and in the ashes of the dried residue of sweat he found carbonate, sulphate, and phosphate of sodium, and some potash, with chloride of sodium, phosphate and carbonate of calcium, and traces of oxide of iron. Urea has also been shown to be an ordinary constituent of the fluid of perspiration.

The ordinary constituents of perspiration, may, according to Gorup-Besanez, be thus summed up: water, fat, acetic, butyric, and formic acid, urea and salts. The principal salts are the chlorides of sodium and potassium, together with, in small quantity, alkaline, and earthy phosphates and sulphates; and, lastly, some oxide of iron. Of these several substances, none, however, need particular consideration, except the carbonic acid and water.

The quantity of *watery vapour* excreted from the skin is on an average between 1½ and 2 lb. daily.

This subject has been estimated very carefully by Lavoisier and Sequin. The latter chemist enclosed his body in an air-tight bag, with a mouth-piece. The bag being closed by a strong band above, and the mouth-piece adjusted and gummed to the skin around the mouth, he was weighed, and then remained quiet for several hours, after which time he was again weighed. The difference in the two weights indicated the amount of loss by pulmonary exhalation. Having taken off the air-tight dress, he was immediately weighed again, and a fourth time after a certain interval. The difference between the two weights last ascertained gave the amount of the cutaneous and pulmonary exhalation together; by subtracting from this the loss by pulmonary exhalation alone, while he was in the air-tight dress, he ascertained the amount of cutaneous transpiration. The repetition of these experiments during a long period, showed that, during a state of rest, the average loss by cutaneous and pulmonary exhalation in a minute, is from seventeen to eighteen grains,—the minimum eleven grains, the maximum thirty-two grains; and that of the eighteen grains, eleven pass off by the skin, and seven by the lungs. The maximum loss by exhalation, cutaneous and pulmonary, in twenty-four hours, is about $3\frac{5}{8}$ lb.; the minimum about $1\frac{1}{2}$ lb. Valentin found the whole quantity lost by exhalation from the cutaneous and respiratory surfaces of a healthy man who consumed daily 40,000 grains of food and drink, to be 19,000 grains, or $2\frac{5}{7}$ lb. Subtracting from this, for the pulmonary exhalation, 5,000 grains, and, for the excess of the weight of the exhaled carbonic acid over that of the equal volume of the inspired oxygen, 2,256 grains, the remainder, 11,744 grains, or nearly $1\frac{2}{3}$ lb., may represent an average amount of cutaneous exhalation in the day.

The quantity of watery vapour lost by transpiration, is of course influenced by all external circumstances which affect the exhalation from other evaporating surfaces, such as the temperature, the hygrometric state, and the stillness of the atmosphere. But, of the variations to which it is subject under the influence of these conditions, no calculation has been exactly made.

Neither, until recently, has there been any estimate of the quantity of *carbonic acid* exhaled by the skin on an average, or in various circumstances. Regnault and Reiset attempted to supply this defect, and concluded, from some careful experiments, that the quantity of carbonic acid exhaled from the skin of a warm-blooded animal is about $\frac{1}{50}$ of that furnished by the pulmonary respiration. Dr. Edward Smith's calculation is somewhat less than this; and still more recent experiments (Aubert) appear to prove that the quantity of carbonic acid exhaled by the skin is only $\frac{1}{200}$ to $\frac{1}{150}$ of that which is secreted by the lungs.

The cutaneous exhalation is most abundant in the lower classes of animals, more particularly the naked Amphibia, as frogs and toads, whose skin is thin and moist, and readily permits an interchange of gases between the blood circulating in it and the surrounding atmosphere. Bischoff found that, after the lungs of frogs had been tied and cut out, about a quarter of a cubic inch of carbonic acid gas was exhaled by the skin in eight hours. And this quantity is very large, when it is remembered that a full-sized frog will generate only about half a cubic inch of carbonic acid by his lungs and skin together in six hours (Milne-Edwards and Müller).

The importance of the respiratory function of the skin, which was once thought to be proved by the speedy death of animals whose skins, after removal of the hair, were covered with an impermeable varnish, has been shown by further observations to have no foundation in fact; the immediate cause of death in such cases being the loss of temperature. A varnished animal is said to have suffered no harm when surrounded by cotton wadding, and to have died when the wadding was removed.

Absorption by the skin has been already mentioned, as an instance in which that process is most actively accomplished. Metallic preparations rubbed into the skin have the same action as when given internally, only in a less degree. Mercury applied in this manner exerts its specific influence upon syphilis, and excites salivation; potassio-tartrate of antimony may excite vomiting, or an eruption extending over the whole body; and arsenic may produce poisonous effects. Vegetable matters, also, if soluble, or already in solution, give rise to their peculiar effects, as cathartics, narcotics, and the like, when rubbed into the skin. The effect of rubbing is probably to convey the particles of the matter into the orifices of the glands whence they are more readily absorbed than they would be through the epidermis. When simply left in contact with the skin, substances, unless in a fluid state, are seldom absorbed.

It has long been a contested question whether the skin covered with the epidermis has the power of absorbing water; and it is a point the more difficult to determine because the skin loses water by evaporation. But, from the result of many experiments, it may now be regarded as a well-ascertained fact that such absorption really occurs. M.-Edwards has proved that the absorption of water by the surface of the body may take place in the lower animals very rapidly. Not only frogs, which have a thin skin, but lizards, in which the cuticle is thicker than in

man, after having lost weight by being kept for some time in a dry atmosphere, were found to recover both their weight and plumpness very rapidly when immersed in water. When merely the tail, posterior extremities, and posterior part of the body of the lizard were immersed, the water absorbed was distributed throughout the system. And a like absorption through the skin, though to a less extent, may take place also in man.

Dr. Madden, having ascertained the loss of weight, by cutaneous and pulmonary transpiration, that occurred during half an hour in the air, entered the bath, and remained immersed during the same period of time, breathing through a tube which communicated with the air exterior to the room. He was then carefully dried and again weighed. Twelve experiments were performed in this manner; and in ten there was a gain of weight, varying from 2 scruples to 5 drachms and 4 scruples, or a mean gain of 1 drachm 2 scruples and 13 grains. The loss in the air during the same length of time (half an hour) varied in ten experiments from 2½ drachms to 1 ounce 2½ scruples, or in the mean was about 6½ drachms. So that, admitting the supposition that the cutaneous transpiration was entirely suspended, and estimating the loss by pulmonary exhalation at 3 drachms, there was in these ten experiments of Dr. Madden, an average absorption of 4 drachms 1 scruple and 3 grains, by the surface of the body, during half an hour. In four experiments performed by M. Berthold, the gain in weight was greater than in those of Dr. Madden.

In severe cases of dysphagia, when not even fluids can be taken into the stomach, immersion in a bath of warm water or of milk and water may assuage the thirst; and it has been found in such cases that the weight of the body is increased by the immersion. Sailors also, when destitute of fresh water, find their urgent thirst allayed by soaking their clothes in salt water and wearing them in that state; but these effects may be in part due to the hindrance to the evaporation of water from the skin.

The absorption, also, of different kinds of gas by the skin is proved by the experiments of Abernethy, Cruikshank, Beddoes, and others. In these cases, of course, the absorbed gases com-

bine with the fluids, and lose the gaseous form. Several physiologists have observed an absorption of nitrogen by the skin. Beddoes says, that he saw the arm of a negro become pale for a short time when immersed in chlorine; and Abernethy observed that when he held his hands in oxygen, nitrogen, carbonic acid, and other gases contained in jars, over mercury, the volume of the gases became considerably diminished.

The share which the evaporation from the skin has in the maintenance of the uniform temperature of the body, has been already mentioned (p. 268).

CHAPTER XVI.

THE KIDNEYS AND URINE.

Structure of the Kidneys.

THE kidney is covered on the outside by a rather tough fibrous capsule, which is slightly attached by its inner surface to the proper substance of the organ by means of very fine fibres of areolar tissue and minute blood-vessels. From the healthy kidney, therefore, it may be easily torn off without injury to the subjacent cortical portion of the organ. At the *hilus* or notch of the kidney, it becomes continuous with the external coat of the upper and dilated part of the ureter.

On making a section length-wise through the kidney (fig. 205) the main part of its substance is seen to be composed of two chief portions, called respectively the *cortical* and the *medullary* portion, the latter being also sometimes called the *pyramidal* portion, from the fact of its being composed of about a dozen conical bundles of urine-tubes, each bundle being called a pyramid. The upper part of the duct of the organ, or the *ureter*, is dilated into what is called the *pelvis* of the kidney; and this, again, after separating into two or three principal divisions, is finally subdivided into still smaller portions, varying in number from about 8 to 12, or even more, and called *calyces*. Each of these little calyces or cups, which are often arranged in a double

row, receives the pointed extremity or *papilla* of a *pyramid.* Sometimes, however, more than one papilla is received by a *calyx.*

Fig. 205.*

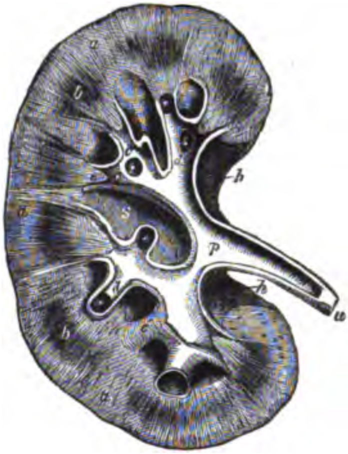


Fig. 206.†

The kidney is a *tubular* gland, and both its cortical and medullary portions are composed essentially of secreting tubes, the *tubuli uriniferi,* which, by one extremity, in the *cortical* portion, end commonly in little saccules containing blood-vessels, called *Malpighian bodies,* and, by the other, open through the *papillæ* into the pelvis of the kidney, and thus discharge the urine which flows through them.

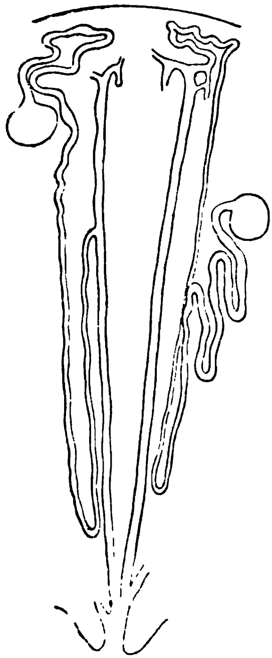
In the pyramids the tubes are chiefly straight—dividing and diverging as they ascend through these into the cortical portion; while in the latter region they spread out more irregularly, and become much branched and convoluted.

* Fig. 205. Plan of a longitudinal section through the pelvis and substance of the right kidney, ½; *a,* the cortical substance; *b, b,* broad part of the pyramids of Malpighi; *c, c,* the divisions of the pelvis named calyces, laid open; *c′,* one of those unopened; *d,* summit of the pyramids or papillæ projecting into calyces; *e, e,* section of the narrow part of two pyramids near the calyces; *p,* pelvis or enlarged divisions of the ureter within the kidney; *u,* the ureter; *s,* the sinus; *h,* the hilus.

† Fig. 206. A. Portion of a secreting tubule from the cortical substance of the kidney. B. The epithelial or gland-cells, more highly magnified (700 times).

The tubuli uriniferi (fig. 206) are composed of a nearly homogeneous membrane, and are lined internally by epithelium. They vary considerably in size in different parts of their course, but are, on an average, about $\frac{1}{500}$ of an inch in diameter. On tracing these tubules upwards from the papillæ, they are found to divide dichotomously as they ascend through the pyramids, and on reaching the bases of the latter, they begin to branch and diverge more widely, and to form by their branches and convolutions the essential part of the *cortical* portion of the organ. At their extremities they become dilated into the *Malpighian capsules*. Until recently, it was believed that the straight tubules in the pyramids branch out and become convoluted immediately on reaching the bases of the pyramids; but between the straight tubes in the pyramids and the convoluted tubes in the *cortical* portion, there has been shown to be a system of tubules of smaller diameter than either, which form intercommunications between the two varieties formerly recognised. These intervening tubules, called the *looped tubes of Henle*, arising from the straight tubes in some part of their course, or being continued from their extremities at the bases of the pyramids, pass down loopwise in the pyramids for a longer or shorter distance,

*Fig. 207.**



* Fig. 207. Diagram of the looped uriniferous tubes and their connection with the capsules of the glomeruli (from Southey, after Ludwig). In the lower part of the figure one of the large branching tubes is shown opening on a papilla; in the middle part two of the looped small tubes are seen descending to form their loops, and re-ascending in the medullary substance; while in the upper or cortical part, these tubes, after some enlargement, are represented as becoming convoluted and dilated in the capsules of glomeruli.

and then, again turning up, end in the convoluted tubes whose extremities are dilated into the *Malpighian capsules* before referred to (fig. 210). On a transverse section of a pyramid (fig. 209), these looped tubes are seen to be of much smaller calibre than the straight ones, which are passing down to open through the papillæ.

The epithelium which lines the urinary tubules, varies somewhat in different parts of their course. In the wider and more tortuous tubules of the cortical portion, it is a pulpy, granular, protoplasmic mass (fig. 208), nucleated but not clearly differentiated into separate spheroidal cells. (C. Ludwig.)

Fig. 208.*

In the straighter and narrower parts of the urinary tubules of the medullary portion, the epithelial lining is more distinctly separated into individual cells, which belong to the columnar or spheroidal type—more commonly the former.

The *Malpighian bodies* (fig. 213) are found only in the cortical part of the kidney. On a section of the organ, some of them are just visible to the naked eye as minute red points; others are too small to be thus seen. Their average diameter is about $\frac{1}{120}$ of an inch. Each of them is composed of the dilated extremity of an urinary tube, or Malpighian *capsule*, enclosing a tuft of blood-vessels.

In connection with these little bodies the general distribution of blood-vessels to the kidney may be here considered.

The renal artery divides into several branches, which, passing in at the hilus of the kidney, and covered by a fine sheath of areolar tissue derived from the capsule, enter the substance of the

* Fig. 208. Section through the cortical canals of a fresh kidney, showing the cloudy or pulpy epithelial layer. The spheroidal nuclei are concealed. In the wider tubules, irregular, in the narrower, regular fissures divide the epithelial mass (C. Ludwig).

organ chiefly in the intervals between the papillæ, and penetrate the cortical substance, where this dips down between the bases

Fig. 209.*

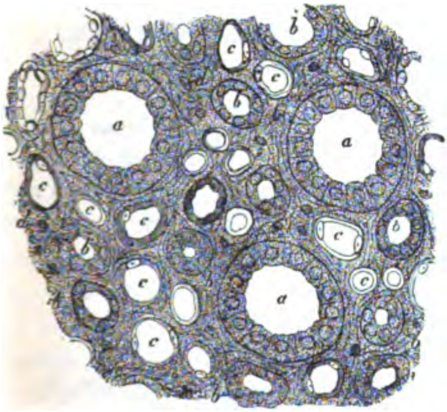
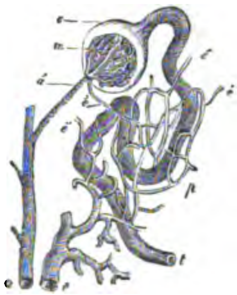


Fig. 210.†



of the pyramids. Here they form a tolerably dense plexus of an arched form, and from this are given off smaller arteries which ultimately supply the Malpighian bodies.

The small *afferent* artery (fig. 210) which enters the Malpighian body by perforating the *capsule*, breaks up in the interior into a dense and convoluted and looped capillary plexus, which is ultimately gathered up again into a single small *efferent* vessel, comparable to a minute vein, which leaves the Malpighian capsule just by the point at which the afferent artery enters it. On leaving, it does not immediately join other small veins as might have been expected, but again breaking up into a network of capillary vessels, is distributed on the exterior of the tubule, from whose dilated end it had just emerged. After this second

* Fig. 209. Transverse section of a renal papilla; *a*, larger tubes or papillary ducts; *b*, smaller tubes of Henle; *c*, blood-vessels, distinguished by their flatter epithelium; *d*, nuclei of the stroma (Kölliker) × 300.

† Fig. 210. Diagram showing the relation of the Malpighian body to the uriniferous ducts and blood-vessels (after Bowman): *a*, one of the interlobular arteries; *a'*, afferent artery passing into the glomerulus; *c*, capsule of the Malpighian body, forming the termination of and continuous with *t*, the uriniferous tube; *e'*, *e'*, efferent vessels which subdivide in the plexus *p*, surrounding the tube, and finally terminate in the branch of the renal vein *e*.

breaking up it is finally collected into a small vein, which, by union with others like it, helps to form the radicles of the renal vein.

Thus, in the kidney, the blood entering by the renal artery traverses *two* sets of capillaries before emerging by the renal vein, an arrangement which may be compared to the *portal* system in miniature.

The tuft of vessels in the course of development is, as it were, thrust into the dilated extremity of the urinary tubule, which finally completely invests it just as the pleura invests the lungs or the tunica vaginalis the testicle. Thus the Malpighian capsule is lined by a parietal layer of squamous cells and a visceral or reflected layer immediately covering the vascular tuft (fig. 211), and sometimes dipping down into its interstices.

Fig. 211.*

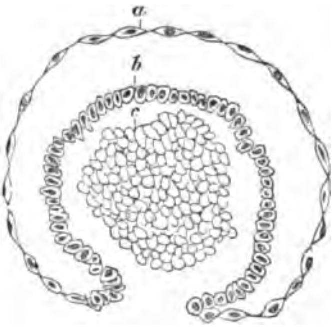
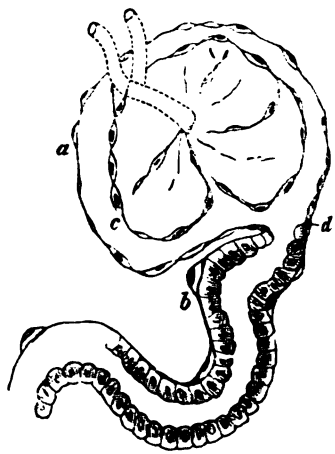


Fig. 212.†

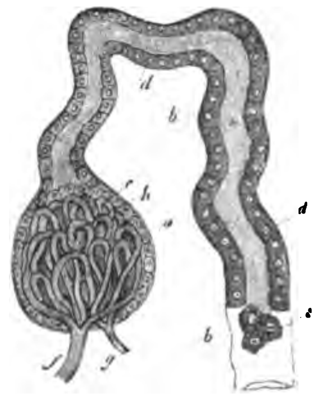


* Fig. 211. Transverse section of a developing Malpighian capsule and tuft (human) × 300. From a fœtus at about the fourth month; *a*, flattened cells growing to form the capsule; *b*, more rounded cells, continuous with the above, reflected round *c*, and finally enveloping it; *c*, mass of embryonic cells which will later become developed into blood-vessels (W. Pye).

† Fig. 212. Epithelial elements of a Malpighian capsule and tuft, with the commencement of a urinary tubule showing the afferent and efferent vessel: *a*, layer of tesselated epithelium forming the capsule; *b*, similar, but rather larger epithelial cells, placed in the walls of the tube; *c*, cells covering the vessels of the capillary tuft; *d*, commencement of the tubule, somewhat narrower than the rest of it (W. Pye).

This reflected layer of epithelium is readily seen in young subjects, but cannot always be demonstrated in the adult. (See figs. 212 and 213.)

Fig. 213.*



Besides the small *afferent* arteries of the Malpighian bodies, there are, of course, others which are distributed in the ordinary manner, for nutrition's sake, to the different parts of the organ; and in the pyramids, between the tubes, there are numerous straight vessels, the *vasa recta*, supposed by some observers to be branches of *vasa efferentia* from Malpighian bodies, and therefore comparable to the venous plexus around the tubules in the *cortical* portion, while others think that they arise directly from small branches of the renal arteries.

Between the tubes, vessels, etc., which make up the substance of the kidney, there exists, in small quantity, a fine matrix of areolar tissue.

The nerves of the kidney are derived from the renal plexus.

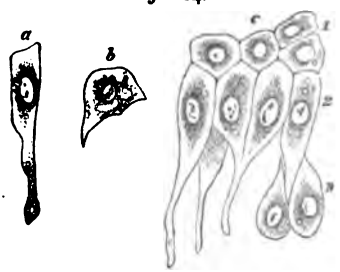
Structure of the Ureters and Urinary Bladder.

The duct of the kidney, or *ureter*, is a tube about the size of a goose-quill, and from a foot to sixteen inches in length, which, continuous above with the pelvis of the kidney, ends below by perforating obliquely the walls of the bladder, and opening on its internal surface. It is constructed of three principal coats, (*a*) an outer, tough, fibrous and elastic coat; (*b*) a middle, muscular coat, of which the fibres are unstriped, and arranged in three layers—the fibres of the central layer being circular, and those

* Fig. 213. Semidiagrammatic representation of a Malpighian body in its relation to the uriniferous tube (from Kölliker) $\frac{300}{1}$. *a*, capsule of the Malpighian body; *d*, epithelium of the uriniferous tube; *e*, detached epithelium; *f*, afferent vessel; *g*, efferent vessel; *h*, convoluted vessels of the glomerulus.

of the other two longitudinal in direction; and (*c*) an internal mucous lining continuous with that of the pelvis of the kidney above, and of the urinary bladder below. The epithelium of all these parts is alike stratified and of a somewhat peculiar form; the cells on the free surface of the mucous membrane being usually spheroidal or polyhedric; while beneath these are conical cells, of which the bases are directed towards the free surface, fitting in beneath the cells of the first row, and the apices are prolonged into processes of various lengths, among which, again, the deepest cells of the epithelium are found spheroidal or irregularly oval (fig. 214).

Fig. 214.*



The Urinary bladder, which forms a receptacle for the temporary lodgment of the urine in the intervals of its expulsion from the body, is more or less pyriform, its widest part, which is situate above and behind, being termed the *fundus;* and the narrow constricted portion in front and below, by which it becomes continuous with the urethra, being called its *cervix* or *neck.*

It is constructed of four principal coats,—*serous, muscular, areolar* or *submucous*, and *mucous.*

(*a*) The *serous* coat, which covers only the posterior and upper half of the bladder, has the same structure as that of the peritoneum, with which it is continuous.

(*b*) The fibres of the muscular coat, which are unstriped, are arranged in three principal layers, of which the external and internal (Ellis) have a general longitudinal, and the middle layer a circular direction. The latter are especially developed around the *cervix* of the organ, and are described as forming a *sphincter vesicæ.*

* Fig. 214. Epithelium of the bladder; *a*, one of the cells of the first row; *b*, a cell of the second row; *c*, cells *in situ*, of first, second, and deepest layers (Obersteiner).

According to Dr. Pettigrew, the muscular fibres of the bladder, like those of the stomach, are arranged not in simple circles, but in figure-of-8 loops.

(*c*) The *areolar* or *submucous* coat is constructed of connective tissue with a large proportion of elastic fibres.

(*d*) The mucous membrane, which is rugose in the contracted state of the organ, does not differ in essential structure from mucous membranes in general. Its epithelium is stratified and closely resembles that of the pelvis of the kidney and the ureter (fig. 214).

The mucous membrane is provided with mucous glands, which are more numerous near the neck of the bladder.

The bladder is well provided with blood- and lymph-vessels, and with nerves. The latter are branches from the sacral plexus (spinal) and hypogastric plexus (sympathetic). A few ganglion-cells are found, here and there, in the course of the nerve-fibres.

Secretion of Urine.

The separation from the blood of the *solids* in a state of solution in the urine is probably effected, like other secretions, by the agency of the epithelial gland-cells of the urine-tubes. The urea and uric acid, and perhaps some of the other constituents existing ready formed in the blood, may need only separation, that is, they may pass from the blood to the urine without further elaboration; but this is not the case with some of the other principles of the urine, such as the acid phosphates and the sulphates, for these salts do not exist as such in the blood, and must be formed by the chemical agency of the cells.

The *watery* part of the urine is probably in part separated by the same structures that secrete the solids, but the ingenious suggestion of Mr. Bowman that the water of the urine is mainly strained off, so to speak, by the Malpighian bodies, from the blood which circulates in their capillary tufts, is exceedingly probable. The process by which the watery portion of the urine is separated from the blood is simple filtration (p. 417) and depends on the considerable blood-pressure in the glomeruli due in part to the fact that the motion of the blood is impeded by

the resistance of *two* sets of capillaries. When, from any cause, such as the impaction of a calculus in the ureter, the pressure of urine in the tubuli increases, the secretion diminishes progressively till it at length ceases entirely, when the blood-pressure within the Malpighian tufts is balanced by that of urine in the tubuli. It seems highly probable that the epithelial cells lining the Malpighian capsules take part also in the secretion of the solids of the urine. We may, therefore, conclude that all parts of the tubular system of the kidney take part in the secretion of the urine as a whole, but that there is a provision also in the arrangement of the vessels in the Malpighian bodies for a more simple draining off of water from the blood when required.

The large size of the renal arteries and veins permits so rapid a transit of the blood through the kidneys, that the whole of the blood is purified by them. The secretion of urine is rapid in comparison with other secretions, and as each portion is secreted, it propels that which is already in the tubes onwards into the pelvis of the kidney. Thence through the ureter the urine passes into the bladder, into which its rate and mode of entrance has been watched in cases of *ectopia vesicæ, i.e.*, of such fissures in the anterior or lower part of the walls of the abdomen, and of the front wall of the bladder, as exposed to view its hinder wall together with the orifices of the ureters. Some good observations on such cases were made by Mr. Erichsen. The urine does not enter the bladder at any regular rate, nor is there a synchronism in its movement through the two ureters. During fasting, two or three drops enter the bladder every minute, each drop as it enters first raising up the little papilla on which, in these cases, the ureter opens, and then passing slowly through its orifice, which at once again closes like a sphincter. In the recumbent posture, the urine collects for a little time in the ureters, then flows gently, and, if the body be raised, runs from them in a stream till they are empty. Its flow is increased in deep inspiration, or straining, and in active exercise, and in fifteen or twenty minutes after a meal.

The same observations, also, showed how fast some substances pass from the stomach through the circulation, and through the vessels of the kidneys.

Ferrocyanide of potassium so passed on one occasion in a minute; vegetable substances, such as rhubarb, occupied from sixteen to thirty-five minutes; neutral alkaline salts with vegetable acids, which were generally decomposed *in transitu*, made the urine alkaline in from twenty-eight to forty-seven minutes. But the times of passage varied much; and the transit was always slow when the substances were taken during digestion.

The urine collecting is prevented from regurgitation into the ureters by the mode in which these pass through the walls of the bladder, namely, by their lying for between half and three-quarters of an inch between the muscular and mucous coats, before they turn rather abruptly forwards, and open through the latter into the interior of the bladder.

Micturition.

The mechanism by which the act of micturition is performed, closely resembles that of defæcation (p. 365). In so far as it is a *voluntary* act, it is performed by means of the abdominal and other expiratory muscles, which in their contraction, as before explained, press on the abdominal viscera, the diaphragm being *fixed*, and cause the expulsion of the contents of those whose sphincter muscles are at the same time relaxed. The muscular coat of the bladder co-operates, in micturition, by reflex *involuntary* action, with the abdominal muscles; and the act is completed by the *accelerator urinæ* which, as its name implies, quickens the stream, and expels the last drops of urine from the urethra.

The Urine.

Healthy urine is a limpid fluid, of a pale yellow or amber colour, with a peculiar faint aromatic odour, which becomes pungent and ammoniacal when decomposition takes place. The urine, though usually clear and transparent at first, often becomes, as it cools, opaque and turbid from the deposition of part of its constituents previously held in solution; and this may be consistent with health, though it is only in disease that, at the temperature of 98° or 100°, at which it is voided, the urine is turbid even when first expelled. Although ordinarily of pale amber colour, yet, consistently with health, the urine

may be nearly colourless, or of a brownish or deep orange tint, and, between these extremes, it may present every shade of colour.

When secreted, and most commonly when first voided, the urine has a distinctly acid reaction in man and all carnivorous animals, the acidity depending on the presence of acid salts, especially phosphate of sodium, and it thus remains till it is neutralized or made alkaline by the ammonia developed in it by decomposition.

In most herbivorous animals the urine is alkaline and turbid. The difference depends, not on any peculiarity in the mode of secretion, but on the differences in the food on which the two classes subsist: for when carnivorous animals, such as dogs, are restricted to a vegetable diet, their urine becomes pale, turbid, and alkaline, like that of an herbivorous animal, but resumes its former acidity on the return to an animal diet; while the urine voided by herbivorous animals, *e.g.*, rabbits, fed for some time exclusively upon animal substances, presents the acid reaction and other qualities of the urine of Carnivora, its ordinary alkalinity being restored only on the substitution of a vegetable for the animal diet (Bernard). Human urine is not usually rendered alkaline by vegetable diet, but it becomes so after the free use of alkaline medicines, or of the alkaline salts with carbonic or vegetable acids; for these latter are changed into alkaline carbonates previous to elimination by the kidneys. Except in these cases, it is very rarely alkaline, unless ammonia has been developed in it by decomposition commencing before it is evacuated from the bladder.

The average *specific gravity* of the human urine is about 1020. Probably no other animal fluid presents so many varieties in density within twenty-four hours as the urine does; for the relative quantity of water and of solid constituents of which it is composed is materially influenced by the condition and occupation of the body during the time at which it is secreted, by the length of time which has elapsed since the last meal, and by several other accidental circumstances. The existence of these causes of difference in the composition of the urine has led to the secretion being described under the three heads of *urina sanguinis*, *urina potus*, and *urini cibi*. The first of these names signifies the urine, or that part of it, which is secreted from the blood at times in which neither food nor drink has been recently taken, and is applied especially to the urine which is evacuated in the morning before breakfast. The term *urina potus* indicates the urine secreted

shortly after the introduction of any considerable quantity of fluid into the body: and the *urini cibi*, the portions secreted during the period immediately succeeding a meal of solid food. The last kind contains a larger quantity of solid matter than either of the others; the first or second, being largely diluted with water, possesses a comparatively low specific gravity. Of these three kinds, the morning urine is the best calculated for analysis, since it represents the simple secretion unmixed with the elements of food or drink; if it be not used, the whole of the urine passed during a period of twenty-four hours should be taken. In accordance with the various circumstances above-mentioned, the specific gravity of the urine may, consistently with health, range widely on both sides of the usual average. The average healthy range may be stated at from 1015 in the winter to 1025 in the summer, and variations of diet and exercise may make as great a difference. In disease, the variation may be greater; sometimes descending, in albuminuria, to 1004, and frequently ascending in diabetes, when the urine is loaded with sugar, to 1050, or even to 1060.

The total quantity of urine passed in twenty-four hours is affected by numerous circumstances. On taking the mean of many observations by several experimenters, Dr. Parkes found that the average quantity voided in twenty-four hours by healthy male adults from 20 to 40 years of age, amounted to 52½ fluid ounces.

The following are the chief conditions which affect the quantity of the secretion:—Blood pressure; Season and Climate; Period of Day; Nervous influences.

1. *Blood-pressure.*

The greater the blood-pressure in the arterial system, and consequently in the renal arteries, the greater, *cæteris paribus*, will be the quantity of urine secreted.

The volume of blood, and therefore the blood-pressure, is increased by the absorption of fluids from the stomach and intestines; and in this way the arterial tension may be very greatly raised. Hence the copious diuresis which rapidly follows on the drinking of large quantities of fluid. The amount of the diuresis thus produced, however, depends of course largely on the excess or deficiency of fluid already in the body. "When the blood and tissues contain their full complement of water, any further potation

results in immediate diuresis, whereby the superabundance is carried off. But when the organs and tissues of the body are craving for more water, a large quantity may be drunk without causing diuresis. The kidneys eliminate water in strict accordance with these conditions—it being an essential and important part of their function to regulate the aqueousness of the blood." (Roberts.)

All the numerous causes which affect the blood-pressure (p. 187) will of course secondarily affect the secretion of urine. Of these the heart's action is among the most important. When its contractions are increased in force (as in cases of hypertrophy) increased diuresis is the result. Similarly, causes which lower the blood-pressure, *e.g.*, enfeebled action of the heart, great loss of blood, &c., greatly diminish the quantity of urine.

2. *Season of the Year.*

It is a matter of familiar observation that much less urine is passed in summer than in winter, and this is doubtless to be attributed to the copious elimination of water by the skin in the form of sweat which occurs in summer, as contrasted with the greatly diminished functional activity of the skin in winter.

Thus we see that in regard to the elimination of water from the system, the skin and kidneys perform similar functions, and are capable to some extent of acting vicariously, one for the other. Their relative activities are inversely proportional to each other.

The quantity of urine passed in summer is smaller, but its specific gravity is usually higher than that of the urine in winter.

3. *Period of Day—Meals, &c.*

On this point some very interesting observations have been made by Dr. Roberts, of Manchester. He compares, not the volumes of urine passed during successive hours, but the quantity of solid constituents contained in these volumes. "A much closer insight into the varying activity of the kidneys is obtained by comparing the quantity of *solid urine* excreted at different periods of the day. The solid matters are much more constant in their quantity than the volume of the urine, which is liable to be greatly affected by potation, perspiration, &c."

The results obtained are summed up by Dr. Roberts as follows:—"The renal excretion is increased after meals and diminished during fasting and sleep. The increase began within the first hour after breakfast, and continued during the succeeding two or three hours; then a diminution set in, and continued until an hour or two after dinner. The effect of dinner did not appear until two or three hours after the meal; and it reached its maximum about the fourth hour. From this period the excretion steadily decreased until bed-time. During sleep it sank still lower, and reached its minimum—being not more than one-third of the quantity excreted during the hours of digestion.

4. *Influence of the Nervous System.*

This is seen in the copious diuresis which occurs often in hysteria, and has been ascertained by experiment.

Injury to a portion of the floor of the fourth ventricle increases the flow of urine.

As in the case of the submaxillary gland, irritation of a cerebro-spinal nerve (pneumogastric in the case of the kidneys) causes dilatation of the blood-vessels and increased secretion, while irritation of the sympathetic (splanchnic) produces an opposite effect.

Chemical Composition of the Urine.

The urine consists of water, holding in solution certain organic and saline matters as its ordinary constituents, and occasionally various matters taken into the stomach as food—salts, colouring matter, and the like. The quantities of the several natural and constant ingredients of the urine are stated somewhat differently by the different chemists who have analysed it; but many of the differences are not important, and the well-known accuracy of the several chemists renders it almost immaterial which of the analyses is adopted. The analysis by A. Becquerel being adopted by Dr. Prout, and by Dr. Golding Bird, will be here employed. (Table I.)

Table II. has been compiled from the observations of Dr. Parkes, and of numerous other authors quoted in his admirable work on the urine.

TABLE I.

Average quantity of each constituent of the Urine in 1000 parts.

Water				967·
Urea				14·230
Uric acid				·468
Colouring matter			inseparable from each other	10·167
Mucus and animal extractive matter				
Salts	Sulphates	Sodium, Potassium		8·135
	Bi-phosphates	Calcium, Sodium, Magnesium, Ammonium		
	Chlorides	Sodium, Potassium		
	Hippurate of sodium			
	Fluoride of potassium			
Silica				traces
				1000·000

TABLE II.

Average quantity of the chief constituents of the Urine excreted in 24 hours by healthy male adults.

Water	52·	fluid ounces.
Urea	512·4	grains.
Uric acid	8·5	"
Hippuric acid, uncertain	probably 10 to 15·	"
Sulphuric acid	31·11	"
Phosphoric acid	45·	"
Chlorine	105·0	"
Chloride of Ammonium	35·25	"
Potash	58·	"
Soda	125·	"
Lime	3·5	"
Magnesia	3·	"
Mucus	7·	"
Extractives { Creatin, Creatinin, Pigment, Xanthin, Hypoxanthin }, Resinous matter, &c.	154·0	"

From these proportions, however, most of the constituents are, even in health, liable to variations. Especially the *water* is so. Its variations in different seasons, and according to the quantity of drink and exercise, have already been mentioned. It is also liable to be influenced by the condition of the nervous system, being sometimes greatly increased in hysteria, and some other nervous affections; and at other times diminished. In some diseases it is enormously increased; and its increase may be either attended with an augmented quantity of solid matter, as in ordinary diabetes, or may be nearly the sole change, as in the affection termed diabetes insipidus. In other diseases, *e.g.*, the various forms of albuminuria, the quantity may be considerably diminished. A febrile condition almost always diminishes the quantity of water; and a like diminution is caused by any affection which draws off a large quantity of fluid from the body through any other channel than that of the kidneys, *e.g.*, the bowels and the skin.

A useful rule for approximately estimating the total solids in any given

specimen of healthy urine is to double the last two figures representing the specific gravity. Thus, in urine of sp. gr. 1025, 2 × 25 = 50 grains of solids, are contained in 1000 grains of the urine.

In using this method it must be remembered that the limits of error are much wider in diseased than in healthy urine.

Urea (CH_4N_2O).—Urea is the principal solid constituent of the urine, forming nearly one-half of the whole quantity of solid matter. It is also the most important ingredient, since it is the chief substance by which the nitrogen of decomposed tissue and superfluous food is excreted from the body. For its removal, the secretion of urine seems especially provided; and by its retention in the blood the most pernicious effects are produced.

Fig. 215.*

Urea, like the other solid constituents of the urine, exists in a state of solution. But it may be procured in the solid state, and then appears in the form of delicate silvery acicular crystals, which, under the microscope, appear as four-sided prisms (fig. 215). It is obtained in this state by evaporating urine carefully to the consistence of honey, acting on the inspissated mass with four parts of alcohol, then evaporating the alcoholic solution, and purifying the residue by repeated solution in water or alcohol, and finally allowing it to crystallise. It readily combines with an acid, like a weak base; and may thus be conveniently procured in the form of a nitrate, by adding about half a drachm of pure nitric acid to double that quantity of urine in a watch glass. The crystals of nitrate of urea are formed more rapidly if the urine have been previously concentrated by evaporation.

Urea is colourless when pure; when impure, yellow or brown: without smell, and of a cooling, nitre-like taste; has neither an acid nor an alkaline re-action, and deliquesces in a moist and warm atmosphere. At 59° F. it requires for its solution less than its weight of water; it is dissolved in all proportions by boiling water; but it requires five times its weight of cold alcohol for its solution. At 248° F. it melts without undergoing decomposition; at a still higher temperature ebullition takes place, and carbonate of ammonia sublimes; the melting mass gradually acquires a pulpy consistence; and, if the heat is carefully regulated, leaves a grey-white powder, cyanic acid.

* Fig. 215. Crystals of Urea.

Urea is identical in composition with cyanate of ammonium, and was first artificially produced by Wohler from this substance. Thus :—

$$\underset{\text{Ammonium Cyanate.}}{NH_4.\ CNO} = \underset{\text{Urea.}}{CH_4N_2O.}$$

The action of heat upon urea in evolving carbonate of ammonia, and leaving cyanic acid, is thus explained. A similar decomposition of the urea with development of carbonate of ammonia ensues spontaneously when urine is kept for some days after being voided, and explains the ammoniacal odour then evolved. It is probable, that this spontaneous decomposition is accelerated by the mucus and other animal matters in the urine, which, by becoming putrid, act the part of a ferment and excite a change of composition in the surrounding compounds. It is chiefly thus that the urea is sometimes decomposed before it leaves the bladder, when the mucous membrane is diseased, and the mucus secreted by it is both more abundant and, probably, more prone than usual to become putrid. The same occurs also in some affections of the nervous system, particularly in paraplegia.

The quantity of urea excreted is, like that of the urine itself, subject to considerable variation. For a healthy adult 500 grains per diem may be taken as a fair average. Its percentage in healthy urine is 1·5 to 2·5. It is materially influenced by diet, being greater when animal food is exclusively used, less when the diet is mixed, and least of all with a vegetable diet. As a rule, men excrete a larger quantity than women, and persons in the middle periods of life a larger quantity than infants or old people (Lecanu).

The quantity of urea excreted by children, relatively to their body-weight, is much greater than in adults. Thus the quantity of urea excreted per kilogram of weight was in a child 0·8 grm.: in an adult only 0·4 grm.

Regarded in this way the excretion of carbonic acid gives similar results, the proportions in the child and adult being as 82 : 34.

The quantity of urea does not necessarily increase and decrease with that of the urine, though on the whole it would seem that whenever the amount of urine is much augmented, the quantity of urea also is usually increased (Becquerel); and it appears from observations of Genth, that the quantity of urea, as of urine, may be especially increased by drinking large quantities of water. In various diseases, as albuminuria, the quantity is

reduced considerably below the healthy standard, while in other affections it is above it.

A convenient apparatus for estimating the quantity of urea in a given sample of urine is that devised by Dr. Russell and Dr. S. H. West.

Urea contains nearly half its weight of nitrogen; hence this gas may be taken as a measure of the urea. A small quantity of urine is mixed with a large excess of solution of hypobromite of soda, which completely decomposes the urea, liberating all the nitrogen in a gaseous form: a gentle heat promotes the reaction. The percentage of urea can of course be readily calculated from the volume of nitrogen evolved from a measured quantity of the urine, but this calculation is avoided by graduating the tube in which the nitrogen is collected with numbers which indicate the corresponding percentage of urea.

The urea appears to be derived from two different sources. That it is derived in part from the unassimilated elements of nitrogenous food, circulating with the blood, is shown in the increase which ensues on substituting an animal or highly nitrogenous for a vegetable diet; in the much larger amount, nearly double, excreted by Carnivora than Herbivora, independent of exercise; and in its diminution to about one-half during starvation, or during the exclusion of non-nitrogenous principles of food. But that it is in larger part derived from the disintegration of the azotized animal tissues, is shown by the fact that it continues to be excreted, though in smaller quantity than usual, when all nitrogenous substances are strictly excluded from the food, as when the diet consists for several days of sugar, starch, gum, oil, and similar non-azotized vegetable substances (Lehmann). It is excreted also, even though no food at all be taken for a considerable time; thus it is found in the urine of reptiles which have fasted for months; and in the urine of a madman, who had fasted eighteen days, Lassaigne found both urea and all the components of healthy urine. Probably all the nitrogenous tissues furnish a share of urea by their decomposition.

It has been commonly taken for granted that the quantity of urea in the urine is greatly increased by active exercise; but numerous observers have failed to detect more than a slight increase under such circumstances; and our notions concerning the relation of this excretory product to the destruction of

muscular fibre, consequent on the exercise of the latter, have lately undergone considerable modification. There is no doubt, of course, that like all parts of the body, the muscles have but a limited term of existence, and are being constantly renewed, at the same time that a part of the products of their disintegration appears in the urine in the form of urea. But the waste is not so fast as it has been frequently supposed to be; and the theory that the amount of work done by the muscle is expressed by the quantity of urea excreted in the urine, and that each act of contraction corresponds to an *equivalent* waste of muscle-structure, is founded on error. (See also Chapter on Motion.)

Urea exists ready-formed in the blood, and is simply abstracted therefrom by the kidneys. It may be detected in small quantity in the blood, and in some other parts of the body, *e.g.*, the humours of the eye (Millon), even while the functions of the kidneys are unimpaired: but when from any cause, especially extensive disease or extirpation of the kidneys, the separation of urine is imperfect, the urea is found largely in the blood and in most other fluids of the body.

Uric Acid ($C_5H_4N_4O_3$).—This substance which was formerly termed lithic acid, on account of its existence in many forms of urinary calculi, is rarely absent from the urine of man or animals, though in the feline tribe it seems to be sometimes entirely replaced by urea (G. Bird).

The proportionate quantity of uric acid varies considerably in different animals. In man, and Mammalia generally, especially the Herbivora, it is comparatively small. In the whole tribe of birds and of serpents, on the other hand, the quantity is very large, greatly exceeding that of the urea. In the urine of granivorous birds, indeed, urea is rarely if ever found, its place being entirely supplied by uric acid.

The quantity of uric acid, like that of urea, in human urine, is increased by the use of animal food, and decreased by the use of food free from nitrogen, or by an exclusively vegetable diet. In most febrile diseases, and in plethora, it is formed in unnaturally large quantities; and in gout it is deposited in, and in the tissues around, joints, in the form of urate of soda, of

which the so-called chalk-stones of this disease are principally composed.

The condition in which uric acid exists in solution in the urine has formed the subject of some discussion, because of its difficult solubility in water.

According to Liebig the uric acid exists as urate of soda, produced, he supposes, by the uric acid, as soon as it is formed, combining with part of the base of the alkaline phosphate of soda of the blood. Hippuric acid, which exists in human urine also, he believes, acts upon the alkaline phosphate in the same way, and increases still more the quantity of acid phosphate, on the presence of which it is probable that a part of the natural acidity of the urine depends. It is scarcely possible to say whether the union of uric acid with the base soda and probably ammonia, takes place in the blood, or in the act of secretion in the kidney: the latter is the more probable opinion; but the quantity of either uric acid or urates in the blood is probably too small to allow of this question being solved.

The source of uric acid is probably in the disintegrated elements of albuminous tissues. The relation which uric acid and urea bear to each other is, however, still obscure. The fact that they often exist together in the same urine, makes it seem probable that they have different origins or different offices to perform; but the entire replacement of either by the other, as of urea by uric acid in the urine of birds, serpents, and many insects, and of uric acid by urea, in the urine of the feline tribe of Mammalia, shows that each alone may discharge all the important functions of the two.

*Fig. 216.**

Owing to its existence in combination in healthy urine, uric acid for examination must generally be precipitated from its bases by a stronger acid. Frequently, however, when excreted in excess, it is deposited in a crystalline form (fig. 216), mixed with large quantities of urate of ammonia or soda. In such cases it may be procured for microscopic examination, by gently warming the portion of urine containing the sediment; this dissolves urate of ammonia and

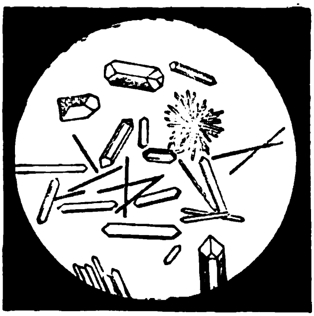
* Fig. 216. Various forms of uric acid crystals.

soda, while the comparatively insoluble crystals of uric acid subside to the bottom.

The most common form in which uric acid is deposited in urine, is that of a brownish or yellowish powdery substance, consisting of granules of urate of ammonia or soda. When deposited in crystals, it is most frequently in rhombic or diamond-shaped laminæ, but other forms are not uncommon (fig. 216). When deposited from urine, the crystals are generally more or less deeply coloured, by being combined with the colouring principles of the urine.

Hippuric Acid ($C_9 H_9 N O_3$) has long been known to exist in the urine of herbivorous animals in combination with soda. Liebig has shown that it also exists naturally in the urine of man, in quantity equal to the uric acid, and Weismann's observations agree with this. It is closely allied to benzoic acid; and this substance when introduced into the system, is excreted by the kidneys as hippuric acid (Ure). Its source is not satisfactorily determined: in part it is probably derived from some constituents of vegetable diet, though man has no hippuric acid in his food, nor, commonly, any benzoic acid that might be converted into it; in part from the natural disintegration of tissues, independent of vegetable food, for Weismann constantly found an appreciable quantity, even when living on an exclusively animal diet.

Fig. 217.*



The nature and composition of the *colouring matter* of urine are involved in some obscurity. It is probably closely related to the colouring matter of the blood.

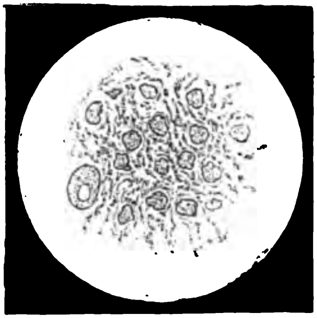
A peculiar substance termed *Indican* has been found by Schenck in the urine. It is not itself pigmentary, though by its decomposition indigo blue and indigo red are produced.

* Fig. 217. Crystals of hippuric acid.

Its presence can usually be detected by adding to a small quantity of urine an equal bulk of hydrochloric acid, and gently heating the solution; on the addition of two or three drops of strong nitric acid a delicate purplish tinge is developed.

The *mucus* in the urine consists principally of the epithelial débris of the mucous surface of the urinary passages. Particles of epithelium, in greater or less abundance, may be detected in most samples of urine, especially if it has remained at rest for some time, and the lower strata are then examined (fig. 218). As urine cools, the mucus is sometimes seen suspended in it as a delicate opaque cloud, but generally it falls. In inflammatory affections of the urinary passages, especially of the bladder, mucus in large quantities is poured forth, and speedily undergoes decomposition. The presence of the decomposing mucus excites (as already stated, p. 464) chemical changes in the urea, whereby ammonia, or carbonate of ammonium, is formed, which, combining with the excess of acid in the super-phosphates in the urine, produces insoluble neutral or alkaline phosphates of calcium and magnesium, and phosphate of ammonium and magnesium. These mixing with the mucus, constitute the peculiar white, viscid, mortar-like substance which collects upon the mucous surface of the bladder, and is often passed with the urine, forming a thick tenacious sediment.

Fig. 218.*



Besides mucus and colouring matter, urine contains a considerable quantity of animal matter, usually described under the obscure name of *extractive*. The investigations of Liebig, Heintz, and others, have shown that some of this ill-defined substance consists of *Creatin* and *Creatinin*, two crystallizable substances derived, probably, from the metamorphosis of mus-

* Fig. 218. Mucus deposited from urine.

cular tissue. These substances appear to be intermediate between the proper elements of the muscles, and, perhaps, of other nitrogenous tissues, and urea: the first products of the disintegrating tissues probably consisting not of urea, but of Creatin and Creatinin, which subsequently are partly resolved into urea, partly discharged, without change, in the urine. The names of some other substances of which there are commonly traces in the urine, will be found in Table II. (p. 462). It has been shown by Scherer that much of the substance classed as extractive matter of the urine, is the peculiar colouring matter, probably derived from the hæmo-globin of the blood.

Saline Matter.—The sulphuric acid in the urine is combined chiefly or entirely with soda and potash: forming salts which are taken in very small quantity with the food, and are scarcely found in other fluids or tissues of the body; for the sulphate, commonly enumerated among the constituents of the ashes of the tissues and fluids are, for the most part or entirely, produced by the changes that take place in the burning. Dr. Parkes, indeed, considers that only about one-third of the sulphuric acid found in the urine is derived directly from the food. Hence the greater part of the sulphuric acid which the sulphates in the urine contain, must be formed in the blood, or in the act of secretion of urine; the sulphur of which the acid is formed being probably derived from the decomposing nitrogenous tissues, the other elements of which are resolved into urea and uric acid. It may be in part derived also, as Dr. Parkes observes, from the sulphur-holding taurin and cystin which can be found in the liver, lungs, and other parts of the body, but not generally in the excretions; and which, therefore, must be broken up. The oxygen is supplied through the lungs, and the heat generated during combination with the sulphur, is one of the subordinate means by which the animal temperature is maintained.

Besides the sulphur in these salts, some also appears to be in the urine, uncombined with oxygen; for after all the sulphates have been removed from urine, sulphuric acid may be formed by drying and burning it with nitre. Mr. Ronalds believes that from three to five grains of sulphur are thus daily excreted.

The combination in which it exists is uncertain: possibly it is in some compound analogous to cystin or cystic oxide (p. 472).

The *phosphoric acid* in the urine is combined partly with the alkalies, partly with the alkaline earths—about four or five times as much with the former as with the latter. In blood, saliva, and other alkaline fluids of the body, phosphates exist in the form of alkaline, or neutral acid salts. In the urine they are acid salts, viz., the phosphates of sodium, ammonium, calcium and magnesium, the excess of acid being, according to Liebig, due to the appropriation of the alkali with which the phosphoric acid in the blood is combined, by the several new acids which are formed or discharged at the kidneys, namely, the uric, hippuric, and sulphuric acids, all of which he supposes to be neutralised with soda.

The presence of the acid phosphates accounts, in great measure, or, according to Liebig, entirely, for the acidity of the urine. The phosphates are taken largely in both vegetable and animal food; some thus taken, are excreted at once; others, after being transformed and incorporated with the tissues. Phosphate of calcium forms the principal earthy constituent of bone, and from the decomposition of the osseous tissue the urine derives a large quantity of this salt. The decomposition of other tissues also, but especially of the brain and nerve-substance, furnishes large supplies of phosphorus to the urine, which phosphorus is supposed, like the sulphur, to be united with oxygen, and then combined with bases. This quantity is, however, liable to considerable variation. Any undue exercise of the brain, and all circumstances producing nervous exhaustion, increase it. The earthy phosphates are more abundant after meals, whether on animal or vegetablé food, and are diminished after long fasting. The alkaline phosphates are increased after animal food, diminished after vegetable food. Exercise increases the alkaline, but not the earthy phosphates (Bence Jones). Phosphorus uncombined with oxygen appears, like sulphur, to be excreted in the urine (Ronalds). When the urine undergoes alkaline fermentation, phosphates are deposited in the form of an *urinary sediment* consisting chiefly of phosphates of ammonium

and magnesium (triple phosphate) (fig. 219). This compound does not, as such, exist in healthy urine. The ammonia is chiefly or wholly derived from the decomposition of urea (p. 469).

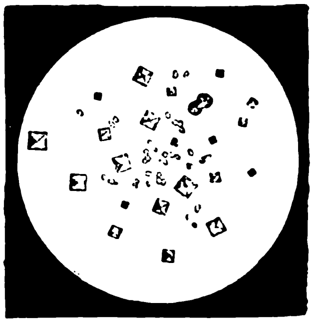
Fig. 219.*

The chlorine of the urine occurs chiefly in combination with sodium, but slightly also with ammonium, and, perhaps, potassium. As the chlorides exist largely in food, and in most of the animal fluids, their occurrence in the urine is easily understood.

Cystin (fig. 220) is an occasional constituent of urine. It resembles taurin in containing a large quantity of sulphur—more than 25 per cent. It does not exist in healthy urine.

Fig. 220.†

Fig. 221.‡



Another common morbid constituent of the urine is oxalic acid, which is frequently deposited in combination with lime (fig. 221) as an urinary sediment. Like cystin, but much more commonly, it is the chief constituent of certain calculi.

* Fig. 219. Urinary sediment of triple phosphates (large prismatic crystals) and urate of ammonia, from urine which had undergone alkaline fermentation.

† Fig. 220. Crystals of cystin.

‡ Fig. 221. Crystals of oxalate of calcium.

A small quantity of gas is naturally present in the urine in a state of solution. It consists chiefly of carbonic acid and nitrogen.

CHAPTER XVII.

THE INCOME AND EXPENDITURE OF THE HUMAN BODY.

From what has been said in Chap. II. on the Relation of Life to other Forces, it will have been gathered that the human body is an energy-transforming machine, absolutely dependent on supplies of potential energy (food and oxygen) for the continuance of its life. So far, it resembles a steam-engine, or other similar apparatus. The products in the two cases, however, may be alike or they may be widely different. The energy by which an arm or leg is moved, is just the same energy as that by which a piston or a wheel is moved, although in one case the transformation of heat into motion is effected by an apparatus for the production of steam, and, in the other by an apparatus called a muscular fibre, of whose *construction* we know nothing. On the other hand, the products may be widely different—and different, not only from anything produced by a steam-engine, but from everything else with which we are acquainted. The state which we call *consciousness*, and the force we call *thought*, are products of a nervous apparatus, as certainly as movement is a product of a muscular apparatus. But in this case we not only know nothing of the *construction* of the apparatus, but are equally ignorant of the nature of the energy produced. The brain is, however, as dependent on supplies of potential energy from the outer world as a muscle or a steam-engine; and we may feel equally certain in its case, as in theirs, that the mind-products of its action are correlated with the physical forces thus brought into connection with it.

So much potential energy is taken into the body from without, and so much active energy is manifested in correlation with it, within. It becomes then an interesting subject of enquiry,—What are the various sources of *Income* for the body? and what is the extent and manner of its *Expenditure?*

The subject may be considered under the following heads. (1). The Evidence and Amount of Expenditure. (2). The Sources and Amount of Income. (3). The Sources and Objects of Expenditure.

1. The *evidence* of Expenditure by the living body is abundantly complete.

From the Lungs there is exhaled every 24 hours,

Of Carbonic Acid, about	15,000 grains
„ Water	5,000 „
Traces of organic matter.	

From the Skin—

Water	11,500 grains
Solid and gaseous matter	250 „

From the Kidneys—

Water	23,000 grains
Organic matter	680 „
Minerals or salines	420 „

From the Intestines—

Water	2,000 „
Various organic and mineral substances .	800 „

In the account of Expenditure, must be reckoned the milk, (during the period of suckling) and the products of secretion from the generative organs (ova, menstrual blood, semen); but, from their variable and uncertain amounts, these cannot be reckoned with the preceding.

Altogether, the Expenditure of the body represented by the sum of these various excretory products amounts every 24 hours to—

Solid and gaseous matter	2–3 lb.
Water (either fluid or combined with the solids and gaseous matter)	5–6 lb.

or, in other words about 3,000 lb. of matter (20 times the weight of a man of average size) are lost from the human body every year.

It should be remembered that the matter thus lost by the body is matter, the chemical attractions of which have been in great part satisfied; and which remains quite useless as food, until its elements have been again separated and re-arranged by members of the vegetable world (pp. 16–19). It is especially instructive to compare the chemical constitution of the products of expenditure, thus separated by the various excretory organs, with that of the sources of income to be immediately considered.

It is evident from these facts that if the human body is to maintain its size and composition, there must be added to it matter corresponding in amount with that which is lost. The income must equal the expenditure.

2. The Income of the body consists partly of *Food* and *Drink*, and partly of *Oxygen*.

Into the stomach there is received daily :—

Solid (chemically dry) food . . .	8,000 grains
Water (as water, or variously combined with solid food)	35,000–40,000 "

By the Lungs there is absorbed daily :—

Oxygen	13,000 "

The average total daily receipts, in the shape of food, drink, and oxygen, correspond therefore, with the average total daily expenditure, as shown by the following table.

Income.		*Expenditure.*	
Solid food	8,000 grains	Lungs	20,000 grains
Water	37,650 "	Skin	11,750 "
Oxygen	13,000 "	Kidneys . . .	24,100 "
		Intestines . . .	2,800 "
	58,650 grains	(Generative and mammary-gland products are supposed to be included.)	
(Or about 8¼ lb.)			
			58,650 grains

These quantities are approximate only. But they may be taken as fair averages for a healthy adult.

The absolute identity of the two numbers (in *grains*) in the two tables is of course diagrammatic. No such exactitude in the account occurs in any living body, in the course of any given twenty-four hours. But any difference which exists between the two amounts of *income* and *expenditure* at any given period, corresponds merely with the slight variations, in the amount of *capital*, (weight of body) to which the healthiest subject is liable.

The chemical composition of the food (p. 274) may be profitably compared with that of the excreta, as before mentioned. The greater part of our food is composed of matter, which contains much potential energy; and in the chemical changes (combustion and other processes), to which it is subject in the body, active energy is manifested.

3. *The Sources and Objects of Expenditure.*—The sources of necessary waste and expenditure in the living body are various and extensive. They may be comprehended under the following heads:—

(1) *Common wear and tear;* such as that to which all structures living and not living, are subjected by exposure and work; but which must be especially large in the soft and easily decaying structures of an animal body.

(2) *Manifestations of Force in the form either of Heat or Motion.* In the former case, (Heat) the combustion must be sufficient to maintain a temperature of about 100° F. throughout the whole substance of the body, in all varieties of external temperature, notwithstanding the large amount continually lost in the ways previously enumerated (p. 268).

In the case of Motion, there is the expenditure involved in (*a*) Ordinary muscular movements, as in Prehension, Mastication, Locomotion, and numberless other ways: (*b*) Various involuntary movements, as in Respiration, Circulation, Digestion, &c.

(3) *Manifestation of Nerve-force;* as in the general regulation of all physiological processes, *e.g.*, Respiration, Circulation, Digestion; and in Volition and all other manifestations of cerebral activity.

(4) *The energy expended in all physiological processes, e.g.*, Nutrition, Secretion, Growth, and the like.

The Total expenditure or manifestation of energy by an animal body can be measured, with fair accuracy; the terms used being such as are employed in connection with other than vital operations (p. 163). All statements, however, must be considered for the present approximate only, and especially is this the case, with respect to the comparative share of expenditure to be assigned to the various objects just enumerated.

The amount of energy daily manifested by the adult human body in (*a*) the maintenance of its temperature; (*b*) in internal mechanical work, as in the movements of the respiratory muscles, the heart, &c.; and (*c*) in external mechanical work, as in locomotion and all other voluntary movements, has been reckoned at about 3,400 foot-tons (p. 163). Of this amount only one-tenth

is directly expended in internal and external mechanical work; the remainder being employed in the maintenance of the body's heat. The latter amount represents the heat which would be required to raise 48·4 lb. of water from the freezing to the boiling point; or, if converted into mechanical power it would suffice to raise the body of a man weighing about 150 lb. through a vertical height of 8½ miles.

To the foregoing amounts of expenditure must be added the quite unknown quantity expended in the various manifestations of nerve-force, and in the work of nutrition and growth (using these terms in their widest sense). By comparing the amount of energy which should be produced in the body from so much food of a given kind, with that which is actually manifested (as shown by the various products of combustion, in the excretions) attempts have been made, indeed, to estimate, by a process of exclusion, these unknown quantities; but all such calculations must be at present considered only very doubtfully approximate.

Among the sources of error in any such calculations must be reckoned, as a chief one, the, at present, entirely unknown extent to which forces external to the body (mainly heat) can be utilised by the tissues. We are too apt to think that the heat and light of the sun are directly correlated, so far as living beings are concerned, with the chemico-vital transformations involved in the nutrition and growth of the members of the vegetable world only. But animals, although comparatively independent of external heat and other forces, probably utilise them, to the degree occasion offers. And although the *correlative* manifestation of energy in the body, due to external heat and light, may still be measured in so far as it may take the form of mechanical work; yet, in so far as it takes the form of expenditure in nutrition or nerve-force, it is evidently impossible to include it by any method of estimation yet discovered; and all accounts of it must be matters of the purest theory.

These considerations may help to explain the apparent discrepancy between the amount of energy which is capable of being produced by the usual daily amount of food, with that which is

actually manifested daily by the body; the former leaving but a small margin for anything beyond the maintenance of heat, and mechanical work.

CHAPTER XVIII.

THE NERVOUS SYSTEM.

The Nervous system consists of two portions or systems, the *Cerebro-spinal* and the *Sympathetic*, each of which (though they have many things in common) possesses certain peculiarities in structure, mode of action, and range of influence.

The *Cerebro-spinal* system includes the Brain and Spinal cord, with the nerves proceeding from them. Its fibres are chiefly, but not exclusively, distributed to the skin and other organs of the senses, and to the voluntary muscles.

The *Sympathetic* Nervous system, is formed by:—(1) A double chain of ganglia and fibres, which extends from the cranium to the pelvis, along each side of the vertebral column, and from which branches are distributed both to the cerebro-spinal system, (all the spinal and many of the cranial nerves) and to other parts of the sympathetic system. With these may be included the small ganglia in connection with those branches of the fifth cerebral nerve which are distributed in the neighbourhood of the organs of special sense: namely, the *ophthalmic*, *otic*, *spheno-palatine*, and *submaxillary* ganglia. (2) Various ganglia and plexuses of nerve-fibres which give off branches to the thoracic and abdominal viscera, the chief of such plexuses being the Cardiac, Solar, and Hypogastric; but in intimate connection with these are many secondary plexuses, as the aortic, spermatic, and renal plexus, &c. To these plexuses, fibres pass from the præ-vertebral chain of ganglia, as well as from cerebro-spinal nerves. (3) Various ganglia and plexuses in the substance of many of the viscera, as stomach, intestines, urinary bladder, and others. These, which are, for the most part, microscopic, also freely communicate with other parts of the sympathetic system, as well as, to some extent, with the cerebro-spinal. (4) By many,

the ganglia on the posterior roots of the spinal nerves, on the glossopharyngeal and pneumogastric, and on the sensory root of the fifth cerebral nerve (Gasserian ganglian), are also included as sympathetic-nerve structures.

Elementary Structures of the Nervous System.

The organs both of the Cerebro-spinal and Sympathetic nervous systems are composed of two structural elements—*cells* and *fibres*. The cells are collected in masses, and are always mingled, more or less, with fibres; such a collection of cellular and fibrous nerve-structure being termed a *nerve-centre*. The fibres, besides entering into the composition of nerve-centres, form by themselves, the *nerves*, which connect the various centres, and are distributed in the several parts of the body.

Functionally, nerve-cells and nerve-fibres differ in this important respect, that the former *generate* and *conduct* nerve-force, while the latter merely *conduct* it. The difference may be compared to that which exists in a telegraphic apparatus, between the galvanic battery and the wires: the former generating and conducting electricity, and the latter merely conducting it.*

Structure of Nerve-Fibres.

Nerves are constructed of minute fibres or tubules full of nervous matter, arranged in parallel or interlacing bundles, which bundles are connected by intervening connective tissue, in which their principal blood-vessels ramify. A layer of areolar or of strong fibrous tissue, also surrounds the whole nerve, and forms a sheath for it. In most nerves, two kinds of fibres are mingled; those of one kind being most numerous in, and characteristic of, nerves of the Cerebro-spinal system; those of the other, most numerous in nerves of the Sympathetic system.

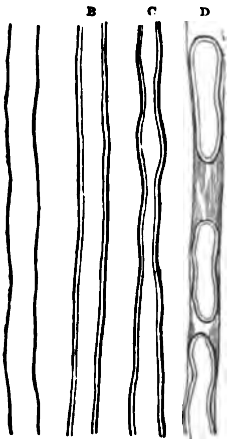
The fibres of the first kind (*white* or *medullated* fibres) consist of tubules of a pellucid, simple membrane (primitive nucleated sheath or *neurilemma*). By the application of nitrate of silver,

* The term generation of nerve or electric force is used for convenience. The sense in which it should be used is illustrated in Chapter II.

this delicate and apparently structureless tubular membrane has been shown to consist of flattened, nucleated endothelial cells. It is absent in the nerve-fibres of the brain and spinal cord.

Within the neurilemma is the proper nerve substance, consisting of transparent, oil-like, and apparently homogeneous material, which gives to each fibre the appearance of a fine glass tube filled with a clear transparent fluid (fig. 222, A). This simplicity of composition is, however, only apparent in the fibres of a perfectly fresh nerve; for, shortly after death, they undergo changes which show that their contents are composed of two different materials. The internal or central part, occupying the axis of the tube (*axis-cylinder*), becomes greyish, while the outer, or cortical portion (*white substance of Schwann*), becomes opaque and dimly granular or grumous, as if from a kind of coagulation. At the same time, the fine outline of the previously transparent cylindrical tube is exchanged for a dark double contour (fig. 222, B), the outer line being formed by the sheath of the fibre, the inner by the margin of curdled or coagulated medullary substance. The granular material shortly collects into little masses, which distend portions of the tubular membrane; while the intermediate spaces collapse, giving the fibres a varicose, or beaded appearance (fig. 222, C and D), instead of the previous cylindrical form. The whole contents of the nerve-tubules are extremely soft, for when subjected to pressure they readily pass from one part of the tubular sheath to another, and

*Fig. 222.**



* Fig. 222. Primitive nerve-tubules. A. A perfectly fresh tubule with a single dark outline. B. A tubule or fibre with a double contour from commencing post-mortem change. C. The changes further advanced, producing a varicose or beaded appearance. D. A tubule or fibre, the central part of which, in consequence of still further changes, has accumulated in separate portions within the sheath (Wagner).

often cause a bulging at the side of the membrane. They also readily escape, on pressure, from the extremities of the tubule, in the form of a grumous or granular material.

The *white substance of Schwann* is the part to which the peculiar white aspect of cerebro-spinal nerves is principally due.

The *axis-cylinder* consists of a large number of primitive *fibrillæ*. This is well shown in the cornea where the axis-cylinders of nerves break up into numerous fibrillæ which go to form terminal networks (see Cornea), and also in the spinal cord where these fibrillæ form a large part of the grey matter.

From various considerations, such as its invariable presence and unbroken continuity in all nerves, though the primitive sheath or the medullary sheath may be absent, there can be little doubt that the axis-cylinder is the conductor of nerve-force, the other parts of the nerve having the subsidiary function of support and possibly of insulation.

Thus in medullated nerve-fibres we must distinguish:—(*a*) The *axis-cylinder* which may be compared to the "core" of copper-wire strands in a submarine telegraph cable. (*b*) The *white substance of Schwann*, sometimes termed the medullary sheath, which may be likened to the insulating layer of gutta percha in a telegraph cable. (*c*) The *primitive* or *nucleated* sheath which, in its relative position, resembles the outer coating of rope.

That there is an essential difference in chemical composition between the central and circumferential parts of a nerve-fibre, *i.e.* between the axis-cylinder and the medullary sheath, has been clearly shown by Messrs. Lister and Turner. Their observations, founded on Mr. Lockhart Clarke's method of investigating nervous substance by means of chromic acid and carmine, have shown that the axis-cylinder of the nerve-fibre is unaffected by chromic acid, but imbibes carmine with great facility, while the medullary sheath is rendered opaque and brown and laminated by chromic acid, but is entirely untinged by the carmine. From this difference in their chemical behaviour, the central and circumferential portions of the nerve-fibres are readily distinguished on microscopic examination, the former being indicated by a bright red carmine-coloured point, the latter by a pale ring surrounding it.

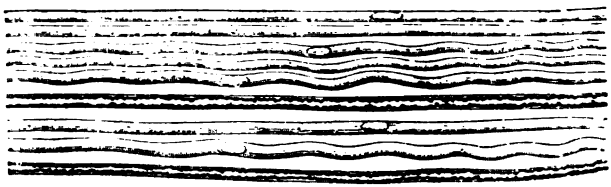
The *size* of the nerve-fibres varies, and the same fibres do not preserve the same diameter through their whole length, being largest in their course within the trunks and branches of the

nerves, in which the majority measure from $\frac{1}{2000}$ to $\frac{1}{3000}$ of an inch in diameter. As they approach the brain or spinal cord, and generally also in the tissues in which they are distributed, they gradually become smaller. In the grey or vesicular substance of the brain or spinal cord, they generally do not measure more than from $\frac{1}{10000}$ to $\frac{1}{14000}$ of an inch.

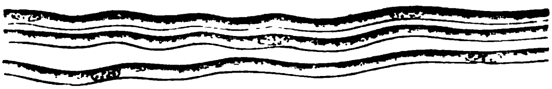
The fibres of the second kind (*grey* or *non-medullated* fibres) (fig. 223), which constitute the whole of the branches of the olfactory nerves, the principal part of the trunk and branches of the sym-

Fig. 223.*

A



B



pathetic nerves, and are mingled in various proportions in the cerebro-spinal nerves, differ from the preceding, chiefly in their fineness, being only about ½ or ⅓ as large in their course within the trunks and branches of the nerves; in the absence of the double contour; in their contents being apparently uniform; and in their having, when in bundles, a yellowish grey hue instead of the whiteness of the cerebro-spinal nerves. These peculiarities depend on their not possessing the outer layer of white or medullary nerve-substance; their contents being composed exclusively of the substance corresponding with the central portion, or axis-cylinder, of the larger fibres. Yet, since many

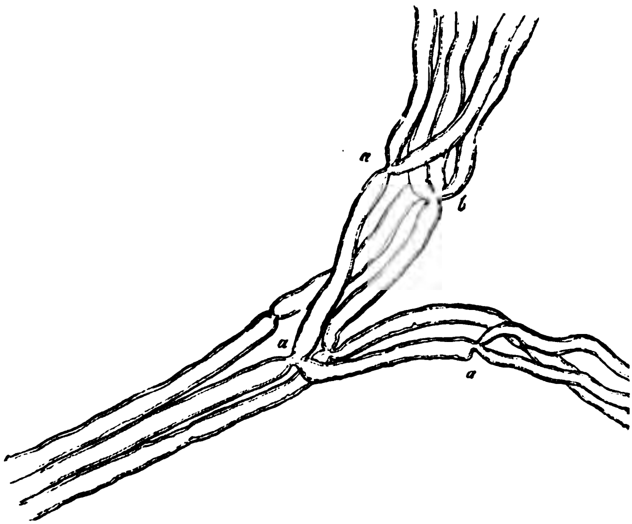
* Fig. 223. Grey, pale, or gelatinous nerve-fibres, magnified between 400 and 500 diameters. A. From a branch of the olfactory nerve of the sheep; *a*, *a*, two dark-bordered or white fibres from the fifth pair, associated with the pale olfactory fibres. B. From the sympathetic nerve. (Max Schultze.)

nerve-fibres may be found which appear intermediate in character between these two kinds, and since the large fibres, as they approach both their central and their peripheral end, gradually diminish in size, and assume many of the other characters of the fine fibres of the sympathetic system, it is not necessary to suppose that there is any material difference in the two kinds of fibres.

It is worthy of note, that, in the fœtus, at an early period of development, all nerve-fibres are non-medullated.

Every nerve-fibre in its course proceeds uninterruptedly from its origin in a nerve-centre to near its destination, whether this

*Fig. 224.**



be the periphery of the body, another nervous centre, or the same centre whence it issued.

Bundles, or fasciculi of fibres, run together in the nerves, but merely lie in apposition with each other; they do not unite: even when the fasciculi anastomose, there is no *union* of fibres.

* Fig. 224. Small branch of a muscular nerve of the frog, near its termination, showing divisions of the fibres. *a*, into two; *b*, into three; magnified 350 diameters (Kölliker).

but only an *interchange* of fibres between the anastomosing fasciculi. Although each nerve-fibre is thus single and undivided through nearly its whole course, yet as it approaches the region in which it terminates, individual fibres break up into several subdivisions (fig. 224) before their final ending in the different fashions to be immediately described. The white or *medullated* nerve-fibres, moreover, lose their medullary sheath or white substance of Schwann before their final distribution, and acquire the characters more or less of the grey or non-medullated fibres.

At certain parts of their course, nerves form *plexuses*, in which they anastomose with each other, and interchange fasciculi, as in the case of the brachial and lumbar plexuses. The objects of such interchange of fibres are, (*a*), to give to each nerve passing off from the plexus, a wider connection with the spinal cord than it would have if it proceeded to its destination without such communication with other nerves. Thus, each nerve by the wideness of its connections, is less dependent on the integrity of any single portion, whether of nerve-centre or of nerve-trunk, from which it may spring. By this means, also, (*b*), each part supplied from a plexus has wider relations with the nerve-centres and more extensive sympathies; and, by means of the same arrangement, as Sir W. Gull has suggested, groups of muscles may be associated for combined actions; every member of the group receiving motor filaments from the same parts of the nerve-centre. (*c*) By a plexiform distribution of fibres to any given part, say of a limb, the part is less dependent upon the integrity of any one nerve (p. 494). (*d*) A plexus is frequently the means by which *centripetal* and *centrifugal* fibres are conveniently mingled for distribution, as in the case of the pneumogastric nerve, which receives motor filaments, near its origin, from the spinal accessory.

The *terminations* of nerve-fibres may be considered under the heads of their *central*, and their *peripheral* terminations.

The *peripheral* termination of nerve-fibres has been always the subject of considerable discussion and doubt. The following are the chief modes of ending of nerve-fibres in the parts they supply.

1. In fine networks or plexuses; examples of this are found in the distribution of nerves in muscles, in mucous and serous membranes, and in the anterior epithelium of the cornea. 2. In special terminal organs, called *touch-corpuscles* (fig. 197), *end-bulbs* (fig. 198), and *Pacinian bodies* (figs. 225, 226). 3. In

*Fig. 225.**

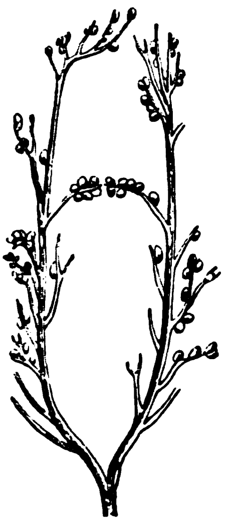


Fig. 226.†

cells; as in the eye and internal ear, and some other parts. 4. In free ends; as from the fine plexuses in muscles (Kölliker). 5. In muscles, a peculiar termination of nerves in small bodies called *motorial end-plates*, has been described by Rouget and others. These small bodies, varying from $\frac{1}{5000}$ to $\frac{1}{350}$ of an inch in diameter, are fixed to the muscular fibres, one for each, and to them the extremity of the minute branch of nerve-fibre

* Fig. 225. Extremities of a nerve of the finger with Pacinian corpuscles attached, about the natural size (adapted from Henle and Kölliker).

† Fig. 226. A magnified view of a single Pacinian corpuscle, showing its laminated structure, and the termination of the nerve-fibre in its central cavity (Bendz).

is attached. These little plates appear to be formed of an expansion of the end of a nerve-fibre with a small quantity of connective tissue.

The Pacinian bodies or corpuscles (figs. 225 and 226), named after their discoverer Pacini, are little elongated oval bodies, situated on some of the cerebro-spinal and sympathetic nerves, especially the cutaneous nerves of the hands and feet; and on branches of the large sympathetic plexus about the abdominal aorta (Kölliker). They often occur also on the nerves of the mesentery, and are especially well seen in the mesentery of the cat. Each corpuscle is attached by a narrow pedicle to the nerve on which it is situated; is is formed of several concentric layers of fine membrane, with intervening spaces containing fluid; through its pedicle passes a single nerve-fibre, which, after traversing the several concentric layers and their immediate spaces, enters a central cavity, and, gradually losing its dark border, and becoming smaller, terminates at or near the distal end of the cavity, in a knob-like enlargement, or in a bifurcation. The enlargement commonly found at the end of the fibre, is said by Pacini to resemble a ganglion-corpuscle; but this observation has not been confirmed. In some cases two nerves have been seen entering one Pacinian body, and in others a nerve after passing unaltered through one, has been observed to terminate in a second Pacinian corpuscle. The physiological import of these bodies is still obscure.

The *central* termination of nerve-fibres can be better considered after the account of the vesicular nerve-substance.

Effects of Section of Nerves.

If a nerve be divided, the distal (peripheral) segment speedily undergoes fatty degeneration, while the proximal portion, which retains its connection with the nerve-centre, remains longer unaffected; from which it has been argued that the ganglion-cells with which it is connected influence its nutrition (Waller).

Nerve-fibres, after being divided, lose their clearness of outline, the medullary sheath breaks up into short pieces, and finally degenerates into a number of fatty molecules. The axis-cylinders also break down and disappear.

The *vesicular* nervous substance contains, as its name implies, *vesicles* or *corpuscles*, in addition to fibres; and a structure, thus

composed of corpuscles and inter-communicating fibres, constitutes a *nerve-centre*: the chief nerve-centres being the grey matter of the brain and spinal cord, and the various so-called *ganglia*. In the brain and spinal cord a fine stroma of retiform tissue called the *neuroglia* extends throughout both the fibrous and vesicular nervous substance, and forms a supporting and investing framework for the whole.

The *nerve-corpuscles*, which give to the ganglia and to certain parts of the brain and spinal cord the peculiar greyish or reddish-grey aspect by which these parts are characterized, are large, nucleated cells, filled with a finely granular material, some

Fig. 227.*

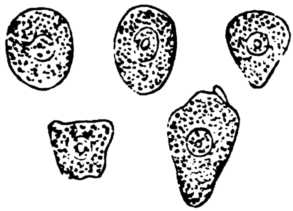
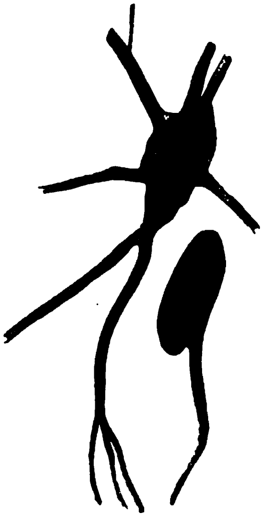


Fig. 228.†



of which is often dark like pigment: the nucleus, which is vesicular, containing a nucleolus (fig. 227). Besides varying much in shape, partly in consequence of mutual pressure, they present such other varieties as make it probable either that there are two different kinds, or that, in the stages of their development, they pass through very different forms. Some of them are small, generally spherical or ovoid, and have a regular

* Fig. 227. Nerve-corpuscles from a ganglion. In one a second nucleus is visible. In several the nucleus contains one or two nucleoli (Valentin).

† Fig. 228. Stellate or caudate nerve-corpuscles, with tubular processes issuing from them. Besides being filled with granular material, continuous with the contents of the processes, the corpuscles contain black pigment (Hannover).

uninterrupted outline (fig. 227). These *simple* nerve-corpuscles are most numerous in the sympathetic ganglia; each is enclosed in a nucleated sheath (fig. 233). Others, which are called *caudate* or *stellate nerve-corpuscles* (fig. 228), are larger, and have one, two, or more long processes issuing from them, the cells being called respectively *unipolar*, *bipolar*, or *multipolar;* which processes often divide and subdivide, and appear tubular, and filled with the same kind of granular material that is contained within the corpuscle. Of these processes some appear to taper to a point and terminate at a greater or less distance from the corpuscle; some appear to anastomose with similar offsets from other corpuscles; while others are continuous with nerve-fibres, the prolongation from the cell by degrees assuming the characters of the nerve-fibre with which it is continuous.

That process of a nerve-cell which becomes continuous with a nerve-fibre is always unbranched, as it leaves the cells. It at first has all the characters of an axis-cylinder, but soon acquires a medullary sheath and then may be termed a nerve-fibre. This continuity of nerve-cells and fibres may be readily traced out in the anterior cornua of the grey matter of the spinal cord.

In many large branched nerve-cells a distinctly fibrillated appearance is observable; the fibrillæ are probably continuous with those of the axis-cylinder of a nerve.

Functions of Nerve-Fibres.

When a cerebro-spinal nerve-fibre is irritated in the living body as by pinching, or by heat, or by electrifying it, there is, under ordinary circumstances, one of two effects,—either there is pain, or there is twitching of one or more muscles to which the nerve distributes its fibres. From various considerations (to be afterwards explained, p. 493) it is certain that pain is always the result of a change in the nerve-cells of the Brain. Therefore, in such an experiment as that referred to, it seems to the experimenter that the irritation of the nerve-fibre is *conducted* in one of two directions, *i.e.*, either to the brain (*central termination of the fibre*), when there is pain, or to a muscle (*peripheral termination*) when there is movement.

The effect of this simple experiment is a type of what always occurs when nerve-fibres are engaged in the performance of their functions. The result of stimulating them, which roughly imitates what happens naturally in the body, is found to occur at one or other of their extremities, central or peripheral, never at both; and in accordance with this fact, and because, for any given nerve-fibre, the result is always the same, nerves are commonly classed as *sensory* or *motor;* the corresponding terms *centripetal* and *centrifugal* being often employed instead, for a reason which will subsequently appear (p. 490).

It may be well to state, in order to avoid confusion, that the apparent conduction in *both* directions, which seems to occur when a nerve, say the ulnar or median, is irritated, depends on the fact that both motor and sensory *fibres* are bound up together in the same *nerve-trunks*—an arrangement which, for medium-sized and large nerves, is the rule rather than the exception.

Microscopic examination fails to discover the slightest difference between motor and sensory nerve-fibres, and the question therefore, naturally arises whether the conduction of a stimulus in one direction only, is not rather apparent than real, the difference in the result being due to the different connections of the two kinds of nerve-fibres respectively at their extremities. In other words, when the stimulation of a nerve-fibre causes pain, the result is due to its *central* extremity being in connection with structures which alone can give rise to the sensation, while its *peripheral* extremity, although the stimulus is equally conducted to it, has no connection with a structure which can respond to the irritation in any manner sensible to the observer. So, when motion is the result of a like irritation, it is because the *peripheral* extremity of the nerve-fibre is in connection with muscles which will respond by contracting, while its *central* extremity, although equally stimulated, has no means of showing the fact by any evident result.

That this is the true explanation is made highly probable, not merely by the absence of any structural differences in the two kinds of nerve-fibre, but also by the fact, proved by direct experiment, that if a centripetal nerve (gustatory) be divided, and its

central portion be made to unite with the distal portion of a divided motor nerve (hypoglossal) the effect of irritating the former after the parts have healed, is to excite contraction in the muscles supplied by the latter. (Philippeaux and Vulpian).

Moreover it has been shown that the effects of an electric current on a nerve-trunk are conducted equally well in both directions.

Classification of Nerve-Fibres.

Nerves are classified as follows:—1. Centripetal, afferent, or sensory. 2. Centrifugal, efferent, or motor. 3. Intercentral.

The terms *centripetal* or *afferent*, and *centrifugal* or *efferent* are frequently employed in connection with nerve-fibres in lieu of the corresponding terms *sensory* and *motor*, because the result of stimulating a nerve of the former kind is not *always* the production of pain or other form of sensation, nor is motion the *invariable* result of stimulating the latter.

Conduction in *centripetal* nerves may cause (*a*) pain, or some other kind of sensation; or (*b*) reflex action; or (*c*) inhibition, or restraint of action (p. 189).

Conduction in *centrifugal* nerves may cause (*a*) contraction of muscle (p. 495), (the nerves being in this case termed *motor*); or (*b*) it may influence nutrition (*trophic* nerves) (p. 403); or (*c*) may influence secretion (*secretory* nerves) (p. 289).

The term *intercentral* is applied to those nerve-fibres which connect more or less distinct nerve-centres, and may, therefore, be said to have no *peripheral* distribution, in the ordinary sense of the term.

Laws of Conduction in Nerve-fibres.

Nerve-fibres possess no power of generating force in themselves, or of originating impulses to action: for the manifestation of their peculiar endowments they require to be stimulated. They possess a certain property of conducting impressions, a property which has been named excitability or irritability; but this is never manifested till some stimulus is applied. Thus, under ordinary circumstances, nerves of sensation are stimulated by external objects acting upon their extremities; and nerves of

motion by the will, or by some force generated in the nervous centres. But almost all things that can disturb the nerves from their passive state act as stimuli, and agents the most dissimilar produce the same kind, though not the same degree of effect.

Thus—mechanical, chemical, electric, and thermal stimuli, when applied to parts endowed with sensation, or to sensory nerves (the connection of the latter with the brain being uninjured), all cause sensations, and, when applied to the nerves of muscles, all excite contraction.

Mechanical, chemical, or any other irritation, when so violent as to injure the texture of the primitive nerve-fibres, deprives the centripetal nerves of their power of producing sensations when irritation is again applied at a point more distant from the brain than the injured spot; and in the same way, no irritation of a motor nerve will excite contraction of the muscle to which it is distributed, if the nerve has been compressed and bruised between the point of irritation and the muscle; the effect of such an injury being the same as that of division.

It is a law of action in all nerve-fibres, and corresponds with the continuity and simplicity of their course, that an impression made on any fibre, is simply and uninterruptedly transmitted along it, without being imparted or diffused to any of the fibres lying near it. In other words, all nerve-fibres are mere *conductors* of impressions. Their adaptation to this purpose is, perhaps, due to the contents of each fibre being completely isolated from those of adjacent fibres by the membrane or sheath in which each is enclosed, and which acts, it may be supposed, just as silk, or other non-conductors of electricity do, which, when covering a wire, prevent the electric condition of the wire from being conducted into the surrounding medium.

Nervous force travels along nerve-fibres with considerable velocity. Helmholtz and Baxt have estimated the average rate of conduction in human motor nerves at 111 feet per second: this result agreeing very closely with that previously obtained by Hirsch. Dr. Rutherford's observations agree with those of Von Wittich, that the rate of transmission in sensory nerves is about 140 feet per second.

Of the laws of conduction peculiar to nerves of sensation and of motion respectively, many can be ascertained only by experiments on the roots of the nerves. For it is only at their origin that the nerves of sensation and of motion are distinct; their filaments, shortly after their departure from the nervous centres, are mingled together, so that nearly all nerves, except those of the special senses, consist of both sensitive and motor filaments, and are hence termed mixed nerves.

Centripetal nerves *appear* (p. 488) able to convey impressions only from the parts in which they are distributed, towards the nerve-centre from which they arise, or to which they tend. Thus, when a sensitive nerve is divided, and irritation is applied to the end of the proximal portion, *i.e.*, of the portion still connected with the nervous centre, sensation is perceived, or a reflex action ensues; but, when the end of the distal portion of the divided nerve is irritated, no effect appears.

When an impression is made upon any part of the course of a sensory nerve, the mind may perceive it as if it were made not only upon the point to which the stimulus is applied, but also upon all the points in which the fibres of the irritated nerve are distributed: in other words, the effect is the same as if the irritation were applied to the parts supplied by the branches of the nerve. When the whole trunk of the nerve is irritated, the sensation is felt at all the parts which receive branches from it; but when only individual portions of the trunk are irritated, the sensation is perceived at those parts only which are supplied by the several portions. Thus, if we compress the ulnar nerve where it lies at the inner side of the elbow-joint, behind the internal condyle, we have the sensation of "pins and needles," or of a shock, in the parts to which its fibres are distributed, namely, in the palm and back of the hand, and in the fifth and ulnar half of the fourth finger. When stronger pressure is made, the sensations are felt in the fore-arm also; and if the mode and direction of the pressure be varied, the sensation is felt by turns in the fourth finger, in the fifth, and in the palm of the hand, or in the back of the hand, according as different fibres or fasciculi of fibres are more pressed upon than others.

It is in accordance with this law, that when parts are deprived of sensibility by compression or division of the nerve supplying them, irritation of the portion of the nerve connected with the brain still excites sensations which are felt as if derived from the parts to which the peripheral extremities of the nerve-fibres are distributed. Thus, there are cases of paralysis in which the limbs are totally insensible to external stimuli, yet are the seat of most violent pain, resulting apparently from irritation of the sound part of the trunk of the nerve still in connection with the brain, or from irritation of those parts of the nervous centre from which the sensitive nerve or nerves which supply the paralysed limbs originate.

An illustration of the same law is also afforded by the cases in which division of a nerve for the cure of neuralgic pain is found useless, and in which the pain continues or returns, though portions of the nerve be removed. In such cases, the disease is probably seated nearer the nervous centre than the part at which the division of the nerve is made, or it may be in the nervous centre itself. In the same way may be explained the fact, that when part of a limb has been removed by amputation, the remaining portions of the nerves may give rise to sensations which the mind refers to the lost part. When the stump is healed, the sensations which we are accustomed to have in a sound limb are still felt; and tingling and pains are referred to the parts that are lost, or to particular portions of them, as to single toes, to the sole of the foot, to the dorsum of the foot, etc.

But (as Volkmann shows) it must not be assumed, as it often has been, from these examples, that the mind has no power of discriminating the very point in the length of any nerve-fibre to which an irritation is applied. Even in the instances referred to, the mind perceives the pressure of a nerve at the point of pressure, as well as in the seeming sensations derived from the extremities of the fibres: and in stumps, pain is felt in the stump, as well as, seemingly, in the parts removed. It is not quite certain whether those sensations are perceived by the nerve-fibres which are on their way to be distributed elsewhere,

or by the sentient extremities of nerves which are themselves distributed to the many trunks of the nerves, the *nervi nervorum*. The latter is the more probable supposition.

The habit of the mind to refer impressions received through the sensory nerves to the parts from which impressions through those nerves are, or were, commonly received, is further exemplified when the relative position of the peripheral extremities of sensitive nerves is changed artificially, as in the transposition of portions of skin. When in the restoration of a nose, a flap of skin is turned down from the forehead and made to unite with the stump of the nose, the new nose thus formed has, as long as the isthmus of skin by which it maintains its original connections remains undivided, the same sensations as if it it were still on the forehead. In other words, when the nose is touched, the patient feels the impression as if it were made on the forehead. When the communication of the nervous fibres of the new nose with those of the forehead is cut off by division of the isthmus of skin, the sensations are no longer referred to the forehead; the sensibility of the nose is at first absent, but is gradually developed.

When, in a part of the body which receives two sensory nerves, one is paralysed, the other may or may not be inadequate to maintain the sensibility of the entire part; the extent to which the sensibility is preserved corresponding probably with the number of the fibres unaffected by the paralysis. There are instances in which the trunk of the chief sensory nerve supplied to a part having been divided, the sensibility of the part is still preserved by intercommunicating fibres from a neighbouring nerve-trunk. Thus, a case is related by Mr. Savory in which, after excision of a portion of the musculo-spiral nerve, the sensibility of some of the parts supplied by it, although impaired, was not altogether lost, probably on account of those fibres from the external cutaneous nerve which are mingled with the radial branch of the musculo-spiral. One of the uses of a nervous plexus (p. 484) is here well illustrated.

The laws of conduction in the nerves of special sense—olfactory, optic, auditory, gustatory—resemble in many aspects those of conduction in the nerves of common sensation, just described. Thus the effect is always *central*; stimulation of the trunk of the nerve produces the same effect as that of its extremities, and if the nerve be severed, it is the central and not the peripheral extremity which responds to irritation, although the sensation is

referred to the periphery. There are, however, certain peculiarities in the effects. Thus the various stimuli, which might cause, through an ordinary sensitive nerve, the sense of pain, would, if applied to the optic nerve, cause a sensation as of flashes of light; if applied to the olfactory, there would be a sense as of something smelt. And so with the other two.

Hence the explanation of so-called *subjective* sensations. Irritation in the optic nerve, or the part of the brain from which it arises, may cause a patient to believe he sees flashes of light, and among the commonest troubles of the nerves of special sense, is the distressing noise in the head (*tinnitus aurium*), which depends on some unknown stimulation of the auditory nerve or centre quite unconnected with external sounds.

Several of the laws of action in *motor nerves* present a remarkable contrast with the foregoing. Thus—the effect of applying a stimulus to the motor nerve is always noticeable, at the peripheral extremity, in the contraction of muscles supplied by it; no effect, as pain or any other kind of sensation, being observable. If a motor nerve be severed, the contrast with a sensitive nerve is equally marked. While irritation of the distal portion causes contraction of muscle as before, no effect whatever is produced by stimulating that part of the nerve which is still in direct connection with the nerve-centre.

By mechanical irritation of a motor nerve, contractions are excited in all the muscles supplied by the branches given off by the nerve below the point irritated, and in those muscles alone: the muscles supplied by the branches which come off from the nerve at a higher point than that irritated, are not directly excited to contraction. And it is from the same fact that, when a motor nerve enters a plexus (p. 484) and contributes with other nerves to the formation of a nervous trunk proceeding from the plexus, it does not impart motor power to the whole of that trunk, but only retains it isolated in the fibres which form its continuation in the branches of that trunk.

(For an exception to this rule in the case of *electric* stimulation, see Section on Electricity in Muscle and Nerve.)

Functions of Nerve-Centres.

As already observed (p. 487), the term *Nerve-centre* is applied to all those parts of the nervous system which contain ganglion-corpuscles, or vesicular nerve-substance, *i.e.*, the Brain, Spinal Cord, and the several Ganglia which belong to the Cerebro-spinal and the Sympathetic systems. Each of these nervous centres has a proper range of functions, the extent of which bears a direct proportion to the number of nerve-fibres that connect it with the various organs of the body, and with other nerve-centres; but all *nerve-centres* have certain general properties and modes of action in common, which may be now briefly considered.

The functions of nerve-centres may be classified as follows:—
1. Conduction. 2. Transference. 3. Reflection. 4. Automatic action.

The term *automatic* is here used to indicate *independent* action on the part of the nerve-centre, as distinguished from the actions previously enumerated, which depend on nerve-stimuli brought to the nerve-centre from other parts.

1. *Conduction* in or through *nerve-centres* may be thus simply illustrated. The food in a given portion of the intestines, acting as a stimulus, produces a certain impression on the nerves in the mucous membrane, which impression is conveyed through them to the adjacent ganglia of the sympathetic. In ordinary cases, the consequence of such an impression on the ganglia is the movement by reflex action (p. 369) of the muscular coat of that and the adjacent part of the canal. But if irritant substances be mingled with the food, the sharper stimulus produces a stronger impression, and this is *conducted through* the nearest ganglia to others more and more distant; and, from all these, reflex motor impulses issuing, excite a wide-extended and more forcible action of the intestines. Or even through the sympathetic ganglia, the impression may be further conducted to the ganglia of the spinal nerves, and through them to the spinal cord, whence may issue motor impulses to the abdominal and other muscles, producing cramp. And yet further, the same morbid impression may be conducted

through the spinal cord to the brain, where it may be *felt*. In the opposite direction, mental influence may be conducted from the brain through a succession of nervous centres—the spinal cord and ganglia, and one or more ganglia of the sympathetic—to produce the influence of the mind on the digestive and other organs; altering both the quantity and quality of their secretions.

2. *Transference of nerve-force.*—It has been previously stated that impressions conveyed by any given centripetal nerve-fibre travel uninterruptedly throughout its whole length, and are not communicated to adjacent fibres.

When such an impression, however, reaches a nerve-centre, it may seem to be communicated to another fibre or fibres; as pain or some other kind of sensation may be felt in a part different altogether from that from which, so to speak, the stimulus started. Thus, in disease of the hip, there may be pain in the knee. This apparent change of place of a sensation to a part to which it would not seem properly to belong is termed *transference.*

The *transference of impressions* may be illustrated by the fact just referred to,—the pain in the knee, which is a common sign of disease of the hip. In this case the impression made by the disease on the nerves of the hip-joint is conveyed to the spinal cord; there it is *transferred* to the central ends or connections of the nerve-fibres which are distributed about the knee. Through these the transferred impression is conducted to the brain, which, referring the sensation to the part from which it usually through these fibres receives impressions, feels as if the disease and the source of pain were in the knee. At the same time that it is transferred, the *primary* impression may be also conducted to the brain; and in this case the pain is felt in both the hip and the knee. And so, in whatever part of the respiratory organs an irritation may be seated, the impression it produces, being conducted to the medulla oblongata, is transferred to the central connections of the nerves of the larynx; and thence, being conducted as in the last case to the brain, the latter perceives the peculiar sensation of tickling in the glottis, which excites

the act of coughing. Or, again, when the sun's light falls strongly on the eye, a tickling may be felt in the nose, exciting sneezing.

A greater extent of transference which may be termed *diffusion* or *radiation of impressions*, is shown when an impression received by a nervous centre is diffused to many other parts in the same centre, and produces sensations extending far beyond the part from which the primary impression was derived. Hence, as in the former cases, result various kinds of what have been denominated sympathetic sensations. Sometimes such sensations are referred to almost every part of the body: as in the shock and tingling of the skin produced by some startling noise. Sometimes only the parts immediately surrounding the point first irritated participate in the effects of the irritation; thus, the aching of a tooth may be accompanied by pain in the adjoining teeth, and in all the surrounding parts of the face; the explanation of such a case being, that the irritation conveyed to the brain by the nerve-fibres of the diseased tooth is *radiated* to the central ends of adjoining fibres, and that the mind perceives this secondary impression as if it were derived from the peripheral ends of the fibres. Thus, also, the pain of a calculus in the ureter is diffused far and wide.

From what has been previously said (p. 493) regarding the laws of action in centripetal nerves, it will be seen at once that it is unnecessary to assume any conduction of the stimulus in the course of the nerve-fibres which belong to the part secondarily affected; inasmuch as irritation of their central connections alone would give rise to all the symptoms to be accounted for.

3. *Reflection of Nerve-Stimuli.*—In the cases of *transference* of nerve-force just described, it has been said that all that need be assumed is a communication of the excited condition of a centripetal nerve to other parts of its nerve-centre than that from which it takes its origin. In the case of *reflection*, on the other hand, the stimulus having been conveyed to a nerve-centre by a *centripetal* nerve, is conducted away again by a *centrifugal* nerve, and effects some change—*motor*, *secretory* or *nutritive* (p. 403)

at the peripheral extremity of the latter—the difference in effect depending on the variety of centrifugal nerve secondarily affected. As in transference, the reflection may take place from a certain limited set of centripetal nerves to a corresponding and related set of centrifugal nerves; as when in consequence of the impression of light on the retina, the iris contracts, but no other muscle moves. Or the reflection may extend to widely different parts: as when an irritation in the larynx brings all the muscles engaged in expiration into coincident movement.

Reflex movements, occurring quite independently of sensation, are generally called *excito-motor;* those which are guided or accompanied by sensation, but not to the extent of a distinct perception or intellectual process, are termed *sensori-motor.*

It will be necessary, hereafter, to consider in detail so many of the instances of the reflecting power of the several nervous centres, that it may be sufficient here to mention only the most general rules of *reflex action* :—

(*a*) For the manifestation of every reflex action, three things are necessary; (1), one or more perfect *centripetal* nerve-fibres, to convey an impression: (2), a *nervous centre* for its reception, and by which it may be reflected; (3), one or more *centrifugal* nerve-fibres, along which the impression may be conducted to the muscular or other tissue (p. 490). In the absence of any one of these three conditions, a proper reflex action could not take place; and whenever impressions made by external stimuli on sensitive nerves give rise to motions, these are never the result of the direct reaction of the sensitive and motor fibres of the nerves on each other; in all such cases the impression is conveyed by the sensitive fibres to a nerve-centre, and is therein communicated to the motor fibres.

(*b*) All reflex actions are essentially involuntary, and may be accomplished independently of the will, though most of them admit of being modified, controlled, or prevented by a voluntary effort.

(*c*) Reflex actions performed in health have, for the most part, a distinct purpose, and are adapted to secure some end desirable for the well-being of the body; but, in disease, many of them

are irregular and purposeless. As an illustration of the first point, may be mentioned movements of the digestive canal, the respiratory movements, and the contraction of the eyelids and the pupil to exclude many rays of light, when the retina is exposed to a bright glare. These and all other normal reflex acts afford also examples of the mode in which the nervous centres *combine* and arrange co-ordinately the actions of the nerve-fibres, so that many muscles may act together for the common end. Another instance of the same kind is furnished by the spasmodic contractions of the glottis on the contact of carbonic acid, or any foreign substance, with the surface of the epiglottis or larynx. Examples of the purposeless irregular nature of morbid reflex action are seen in the convulsive movements of epilepsy, and in the spasms of tetanus and hydrophobia.

(*d*) Reflex muscular acts are often more sustained than those produced by the direct stimulus of muscular nerves. The irritation of a muscular organ, or its motor nerve, produces contraction lasting only so long as the irritation continues; but irritation applied to a nervous centre through one of its centripetal nerves, may excite reflex and harmonious contractions, which last some time after the withdrawal of the stimulus (Volkmann).

Reflex actions have been thus conveniently classified by M. Küss :—

1. Reflex actions, in the performance of which, both the centripetal and centrifugal nerves concerned are *cerebro-spinal; e.g.*, deglutition, sneezing, coughing, and, in pathological conditions, tetanus, epilepsy.

2. Reflex actions, in which the centripetal nerve is *cerebro-spinal*, and the centrifugal is *sympathetic*, most often *vaso-motor; e.g.*, secretion of saliva, or gastric juice; blushing or pallor of the skin.

3. Reflex actions, in which the centripetal nerve is of the *sympathetic* system, and the centrifugal is *cerebro-spinal*. The majority of these are pathological, as in the case of convulsions produced by intestinal worms, or hysterical convulsions.

4. Reflex actions, in which both centripetal and centrifugal nerves are of the *sympathetic* system: as, for example, the obscure actions which preside over the secretion of the intestinal fluids, those which unite the various generative functions and many pathological phenomena.

The *laws of reflex action*, derived from experiment and clinical observation, have been thus formulated by Pflüger :—

I. *Law of unilateral reflection.*

A slight irritation of sensory nerves is reflected along the motor nerves of the same region. Thus, if the skin of a frog's foot be tickled on the *right* side, the *right* leg is drawn up.

II. *Law of symmetrical reflection.*

A stronger irritation is reflected, not only on one side, but also along the corresponding motor nerves of the opposite side. Thus, if the spinal cord of a man has been severed by a stab in the back, when one foot is tickled *both* legs will be drawn up.

III. *Law of intensity.*

In the above case, the contractions will be more violent on the side irritated.

IV. *Law of radiation.*

If the irritation (afferent impulse) increases, it is reflected along the motor nerves which spring from points higher up the spinal cord, till at length all the muscles of the body are thrown into action.

Automatism.—The term *automatism* is employed to indicate the origination of nervous impulses in nerve-centres, and their conduction therefrom, independently of previous reception of a stimulus from another part.

It is impossible, in the present state of our knowledge, to say what actions, if any, in the body are really in this sense automatic. A possible example of automatic nerve-action has been already referred to (p. 257); the apparently best examples of such automatism being found, however, in the case of the cerebrum, which will be afterwards considered.

Secondary or acquired reflex actions.

We must carefully distinguish between reflex actions which may be termed *primary*, and those which are *secondary* or *acquired*. As examples of the former class we may cite sucking, contraction of the pupil, drawing up the legs when the toes are tickled, and many others which are performed as perfectly by the infant as by the adult.

The large class of *secondary* reflex actions consists of acts which require for their first performance and many subsequent repetitions an effort of will, but which by constant repetition are habitually though not necessarily performed, mechanically, *i.e.*, without the intervention of consciousness and volition. As instances we may take reading, writing, walking, etc.

In endeavouring to conceive how such complicated actions can be performed without consciousness and will, we must suppose that in the first instance the will directs the nerve-force along

certain channels causing the performance of certain acts; *e.g.*, the various movements of flexion and extension involved in walking. After a time by constant repetition, these routes become, to use a metaphor, well *worn;* there is, as it were, a beaten track along which the nerve-force travels with much greater ease than formerly: so much so that a slight stimulus, such as the pressure of the foot on the ground, is sufficient to start and keep going indefinitely the complex reflex actions of walking during entire mental abstraction, or even during sleep. In such acts as reading, writing, and the like, it would appear as if the will set the necessary reflex machinery going, and that the reflex actions go on uninterruptedly until again interfered with by the will.

Without this capacity possessed by the nervous system of "organizing conscious actions into more or less unconscious ones," education or training would be impossible. A most important part of the process by which these acquired reflex actions come to be performed automatically consists in what is termed *association.* If two acts be at first performed voluntarily in succession, and this succession is often repeated, the performance of the first is at once followed mechanically by the second. Instances of this "force of habit" must be within the daily experience of every one.

Of course it is only such actions as have become entirely reflex that can be performed during complete unconsciousness, as in sleep. Cases of somnambulism are of course familiar to every one, and authentic instances are on record of persons writing and even playing the piano during sleep.

CEREBRO-SPINAL NERVOUS SYSTEM.

The physiology of the cerebro-spinal nervous system includes that of the Spinal cord, Medulla Oblongata, and Brain, of the several nerves given off from each, and of the Ganglia on those nerves.

The Spinal Cord and its Nerves.

The spinal cord is a cylindriform column of nerve-substance connected above with the brain through the medium of the

Fig. 229.*

* Fig. 229. View of the Cerebro-spinal axis of the nervous system (after Bourgery).—The right half of the cranium and trunk of the body has been removed by a vertical section; the membranes of the brain and spinal marrow

medulla oblongata, and terminating below, about the lower border of the first lumbar vertebra, in a slender filament of grey or vesicular substance, the *filum terminale*, which lies in the midst of the roots of many nerves forming the *cauda equina*. The cord is composed of fibrous (white) and vesicular (grey) nervous substance, of which the former is situated externally, and constitutes its chief portion, while the latter occupies its central or axial portion, and is so arranged, that on the surface of a transverse section of the cord it appears like two somewhat crescentic masses connected together by a narrower portion or isthmus (Fig. 230).

Passing through the centre of this isthmus in a longitudinal direction is a minute canal, which is continued through the whole length of the cord, and opens above into the space at the back of the medulla oblongata and pons Varolii, called the fourth ventricle. It is lined by a layer of cylindrical ciliated epithelium.

The spinal cord consists of two exactly symmetrical halves separated anteriorly and posteriorly by a vertical *fissure*, (the posterior fissure being deeper, but less wide and distinct than the anterior,) and united in the middle line by nervous matter which is usually described as forming two commissures—an *anterior* commissure, in front of the central canal, consisting of both white and grey matter, and a *posterior* commissure of grey matter only, behind the central canal (Fig. 230, B). Each half of the spinal cord is marked on the sides (obscurely at the lower part, but distinctly above) by two longitudinal furrows, which divide it into three portions, columns, or tracts, an *anterior*, *middle* or *lateral*, and *posterior*. From the groove between the anterior and lateral columns spring the *anterior roots* of the spinal nerves (B and C, 5); and just in front of the groove between the lateral and posterior column arise the *posterior roots* of the same (B, 6): a pair of roots on each side corresponding to each vertebra (Fig. 229).

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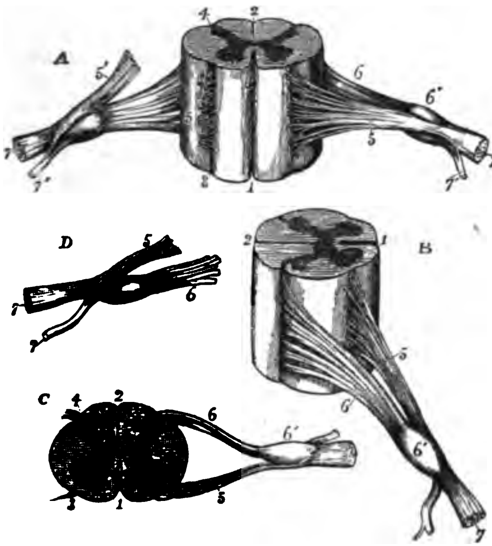
have also been removed, and the roots and first part of the fifth and ninth cranial, and of all the spinal nerves of the right side, have been dissected out and laid separately on the wall of the skull and on the several vertebræ opposite to the place of their natural exit from the cranio-spinal cavity.

White Matter of Spinal Cord.

The fibrous or white part of the cord contains continuations of the innumerable fibres of the spinal nerves issuing from it, or entering it; but it is, probably, not formed of them exclusively;

Fig. 230.*



nor is it a mere trunk, like a great nerve, through which they may pass to the brain.

* Fig. 230. Different views of a portion of the spinal cord from the cervical region, with the roots of the nerves, slightly enlarged. In A, the anterior surface of the specimen is shown; the anterior nerve-root of its right side being divided; in B, a view of the right side is given; in C, the upper surface is shown; in D, the nerve-roots and ganglion are shown from below. 1. the anterior median fissure; 2, posterior median fissure; 3, anterior lateral depression, over which the anterior nerve-roots are seen to spread; 4, posterior lateral groove, into which the posterior roots are seen to sink; 5, anterior roots passing the ganglion; 5′, in A, the anterior root divided; 6, the posterior roots, the fibres of which pass into the ganglion 6′; 7, the united or compound nerve; 7′, the posterior primary branch, seen in A and D to be derived in part from the anterior and in part from the posterior root. (Allen Thomson.)

It is among the most difficult things in structural anatomy to determine the course of individual nerve-fibres, or even of fasciculi of fibres, through even a short distance of the spinal cord; and it is only by the examination of transverse and longitudinal sections through the substance of the cord, such as those so successfully made by Mr. Lockhart Clarke, that we can obtain anything like a correct idea of the direction taken by the fibres of the roots of the spinal nerves within the cord. From the information afforded by such sections it would appear, that, of the root-fibres of the nerves which enter the cord, some assume a transverse, others a longitudinal direction: the fibres of the former pass horizontally or obliquely into the substance of the cord, in which many of them appear to become continuous with fibres entering the cord from other roots; others pass into the columns of the cord, while some perhaps terminate at or near the part which they enter: of the fibres of the second set, which usually first traverse a portion of the grey substance, some pass upwards, and others, at least of the posterior roots, turn downwards, but how far they proceed in either direction, or in what manner they terminate, are questions still undetermined. It is probable that of these latter, many constitute longitudinal commissures, connecting different segments of the cord with each other; while others, probably, pass directly to the brain.

The general rule respecting the size of different parts of the cord appears to be, that the size of each part bears a direct proportion to the size and number of nerve-roots given off from itself, and has but little relation to the size or number of those given off below it. Thus the cord is very large in the middle and lower part of its cervical portion, whence arise the large nerve-roots for the formation of the brachial plexuses and the supply of the upper extremities, and again enlarges at the lowest part of its dorsal portion and the upper part of its lumbar, at the origins of the large nerves which, after forming the lumbar and sacral plexuses, are distributed to the lower extremities. The chief cause of the greater size at these parts of the spinal cord is increase in the quantity of grey matter; for there seems reason to believe that the white or fibrous part of the cord becomes gradually and progressively larger from below upwards, doubtless from the addition of a certain number of upward passing fibres from each pair of nerves.

From careful estimates of the number of nerve-fibres in a transverse section of the cord towards its upper end, and the number entering it by the anterior and posterior roots of each pair of nerves, it has been shown that in the human spinal cord not more than ½ of the total number of nerve-fibres entering the cord through all the spinal nerves are contained in a transverse

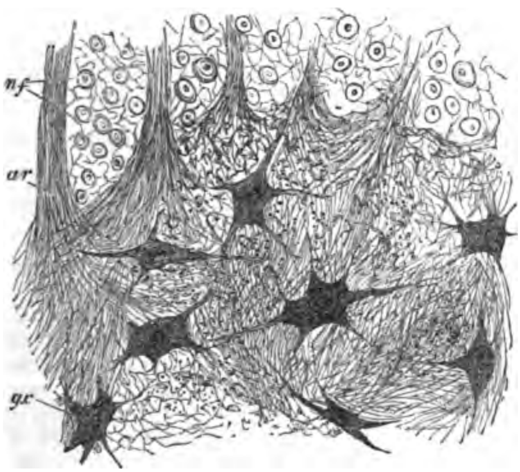
section near its upper end. It is obvious, therefore, that at least ¾ of the nerve-fibres entering it must terminate in the cord itself.

It may be added, however, that there is no sufficient evidence for the supposition that an uninterrupted continuity of nerve-fibres is essential to the conduction of impressions on the spinal nerves to and from the brain: such impressions may be as well transmitted through the nerve-vesicles of the cord as by the nerve-fibres; and the experiments of Brown-Séquard, again to be alluded to, make it probable that the grey substance of the cord is the channel through which sensory impressions are mainly conveyed to the brain.

Grey matter of Spinal Cord.

The grey matter of the cord consists essentially of an extremely delicate network of the primitive fibrillæ of axis-cylinders imbedded in the meshes of an equally delicate connective-tissue (neuroglia), which in some parts is chiefly fibrillated, in others mainly granular and punctiform. It contains numbers of large branched nerve-cells (Fig. 231) which occur chiefly in the three following groups.

Fig. 231.*



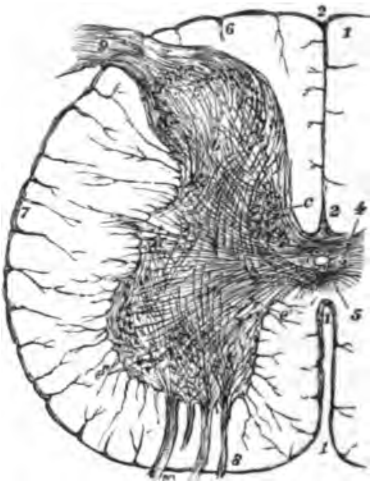
* Fig. 231. Section of grey matter of anterior cornu of calf's spinal cord; *n f*, nerve-fibres of white matter in transverse section, showing axis-cylinder in centre of each; *a r*, anterior roots of spinal nerve passing out through white matter; *g c*, large stellate nerve-cells with nuclei; they are seen imbedded in neuroglia (Schofield).

(*a*) A group in the *anterior cornu*, into many of these cells the fibres of the anterior, motor nerve-roots can be distinctly traced. There can be little doubt that these cells are motor in function.

(*b*) *Tractus intermedio-lateralis* (Lockhart Clarke). A group of nerve-cells midway between the anterior and posterior cornua, near the external surface of the grey matter. It is especially developed in the dorsal and also in the upper cervical region.

(*c*) *Posterior vesicular columns* of Lockhart Clarke and Stilling. These are found in the posterior cornua of grey matter towards the inner surface, extending from the cervical enlargement to the lower end of the cord (Fig. 232).

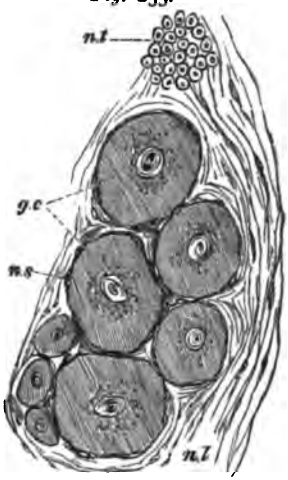
Fig. 232.*



* Fig. 232. Transverse section of half the spinal cord in the lumbar enlargement (semi-diagrammatic). 1, anterior median fissure; 2, posterior median fissure; 3, central canal lined with epithelium; 4, posterior commissure; 5, anterior commissure; 6, posterior column; 7, lateral column; 8, anterior column. The white substance is traversed by radiating trabecula of pia mater. 9, fasciculus of posterior nerve-root entering in one bundle; 10, fasciculi of anterior roots entering in four spreading bundles of fibres. *b*, in the cervix cornu, decussating fibres from the nerve roots and posterior commissure; *c*, posterior vesicular columns of Lockhart Clarke. About half way between the central canal and 7 are seen the group of nerve-cells forming the tractus intermedio-lateralis; *e*, *c*, fibres of anterior roots; *e'*, fibres of anterior roots which decussate in anterior commissure (Allen Thomson). × 6.

The *Nerves of the Spinal Cord* consist of thirty-one pairs, issuing from the sides of the whole length of the cord, their number corresponding with the intervertebral foramina through which they pass. Each nerve arises by two roots, an anterior and posterior, the latter being the larger. The roots emerge through separate apertures of the sheath of dura mater surrounding the cord; and directly after their emergence, where the roots lie in the invertebral foramen, a ganglion is found on the posterior root. The anterior root lies in contact with the anterior surface of the ganglion, but none of its fibres intermingle with those in the ganglion (5, Fig. 230). But immediately beyond the ganglion the two roots coalesce, and by the mingling of their fibres form a compound or mixed spinal nerve, which, after issuing from the intervertebral canal, divides into an anterior and posterior branch, each containing fibres from both the roots (Fig. 230).

Fig. 233.*



The anterior root of each spinal nerve arises by numerous separate and converging fasciculi from the anterior column of the cord; the posterior root by more numerous parallel fasciculi, from the posterior column, or, rather, from the posterior part of the lateral column (Fig. 230), for if a fissure be directed inwards from the groove between the middle and posterior columns, the posterior roots will remain attached to the former. The anterior roots of each spinal nerve consist of centrifugal fibres; the posterior as exclusively of centripetal fibres.

* Fig. 233. Ganglion-cells from spinal ganglion of rabbit; *n, l*, nerve-fibres of posterior root cut longitudinally; *n, t*, nerve-fibres cut transversely; *g, c*, large ganglionc-ells showing granular protoplasm with large nucleus and nucleoli; *n, c*, nucleated sheath surrounding cells. × 250 (Schofield). The figure should be held about 2—3 feet from the eye.

For the knowledge of this important fact, and much of the consequent progress of the physiology of the nervous system, science is indebted to Sir Charles Bell. The fact is proved in various ways. Division of the anterior roots of one or more nerves is followed by complete loss of motion in the parts supplied by the fibres of such roots; but the sensation of the same parts remains perfect. Division of the posterior roots destroys the sensibility of the parts supplied by their fibres, while the power of motion continues unimpaired. Moreover, irritation of the ends of the distal portions of the divided anterior roots of a nerve excites muscular movements; irritation of the ends of the proximal portions, which are still in connection with the cord, is followed by no appreciable effect. Irritation of the distal portions of the divided posterior roots, on the other hand, produces no muscular movements and no manifestation of pain; for, as already stated, sensitive nerves convey impressions only towards the nervous centres: but irritation of the proximal portions of these roots elicit signs of intense suffering. Occasionally, under this last irritation, muscular movements also ensue; but these are either voluntary, or the result of the irritation being reflected from the sensitive to the motor fibres. Occasionally, too, irritation of the distal ends of divided anterior roots elicits signs of pain, as well as producing muscular movements: the pain thus excited is probably the result of *cramp* (Brown-Séquard).

As an example of the experiments of which the preceding paragraph gives a summary account, this may be mentioned: If, in a frog, the three posterior roots of the nerves going to the hinder extremity be divided on the left side, and the three anterior roots of the corresponding nerves on the right side, the left extremity will be deprived of sensation, the right of motion. If the foot of the right leg, which is still endowed with sensation but not with the power of motion, be cut off, the frog will give evidence of feeling pain by movements of all parts of the body except the right leg itself, in which he feels the pain. If, on the contrary, the foot of the left leg, which has the power of motion, but is deprived of sensation, is cut off, the frog does not feel it, and no movement follows, except the twitching of the muscles irritated by cutting them or their tendons.

The *muscular sense* (*i.e.* the power of perceiving the condition of the muscles) with regard to degree of contraction, depends, apparently, on the integrity of the *anterior* roots of the spinal nerves. In a frog in which all the posterior roots have been cut, and in which, therefore, ordinary sensory impressions are not transmitted, the muscular sense remains, as evinced by the animal's power of regulating his movements.

Functions of the Spinal Cord.

The power of the spinal cord, as a nerve-centre, may be arranged under the heads of (1) Conduction; (2) Transference; (3) Reflex action.

(1) *Conduction.* The functions of the spinal cord in relation

to *conduction*, may be best remembered by considering its anatomical connections with other parts of the body (see Fig. 229). From these it is evident that, with the exception of some few filaments of the sympathetic, there is no way by which nerve-impulses can be conveyed from the trunk and extremities to the brain or *vice versâ*, other than that formed by the spinal cord. Through it, the impressions made upon the peripheral extremities or other parts of the spinal sensory nerves are conducted to the brain, where alone they can be *perceived*. Through it, also, the stimulus of the will, conducted from the brain, is capable of exciting the action of the muscles supplied from it with motor nerves. And for all these conductions of impressions to and fro between the brain and the spinal nerves, the perfect state of the cord is necessary; for when any part of it is destroyed, and its communication with the brain is interrupted, impressions on the sensory nerves given off from it below the seat of injury, cease to be propagated to the brain, and the brain loses the power of voluntarily exciting the motor nerves proceeding from the portion of cord isolated from it.

Illustrations of this are furnished by various examples of paralysis, but by none better than by the common paraplegia, or loss of sensation and voluntary motion in the lower part of the body, in consequence of destructive disease or injury of a portion, including the whole thickness, of the spinal cord. Such lesions destroy the communication between the brain and all parts of the spinal cord below the seat of injury, and consequently cut off from their connection with the brain the various organs supplied with nerves issuing from those parts of the cord.

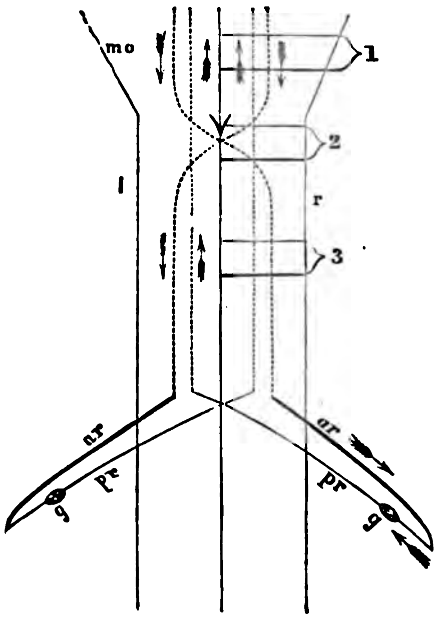
From what has been already said, it will appear probable that the conduction of impressions along the cord is effected (at least, for the most part) through the grey substance, *i.e.*, through the nerve-corpuscles and filaments connecting them. But there is reason to believe that all parts of the cord are not alike able to conduct all impressions; and that, rather, as there are separate nerve-fibres for motor and for sensory impressions, so in the cord, separate and determinate parts serve to conduct always the same kind of impression.

Experiments (chiefly by Brown-Séquard), point to the fol-

lowing conclusions regarding the conduction of sensory and motor impressions through the spinal cord.

It is important to bear in mind that the *grey* matter of the cord, though it conducts impressions giving rise to sensation,

Fig. 234.*



appears not to be sensitive when it is directly stimulated. The explanation probably is, that it possesses no apparatus such as exists at the peripheral terminations of sensory nerves, for the reception of sensory impressions.

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* Fig. 234. The above diagram (after Brown-Séquard) represents the decussation of the conductors for voluntary movements, and those for sensation : *a, r*, anterior roots and their continuations in the spinal cord, and decussation at the lower part of the medulla oblongata, *m o; p r*, the posterior roots and their continuation and decussation in the spinal cord; *g g*, the ganglions of the roots. The arrows indicate the direction of the nervous action; *r*, the right side; *l*, the left side. 1, 2, 3, indicate places of alteration in a lateral half of the spino-cerebral axis, to show the influence on the two kinds of conductors, resulting from section of the cord at any one of these three places.

a. Sensory impressions, conveyed to the spinal cord by root-fibres of the posterior nerves are not conducted to the brain only by the posterior columns of the cord, but pass through them in great part into the central grey substance, by which they are transmitted to the brain (*p r*, fig. 234).

b. The impressions thus conveyed to the grey substance do not pass up to the brain to more than a slight degree, along that half of the cord corresponding to the side from which they have been received, but, almost immediately after entering the cord, cross over to the other side, and along it are transmitted to the brain. There is thus, in the cord itself, an almost complete decussation of sensory impressions brought to it; so that division or disease of one posterior half of the cord (3, fig. 234) is followed by lost sensation, not in parts on the corresponding, but in those of the opposite side of the body.

From the same fact it happens that a longitudinal antero-posterior section of the cord, along its whole length almost completely abolishes sensibility on both sides of the body.

c. The various sensations of touch, pain, temperature, and muscular contraction, are probably conducted along separate and distinct sets of fibres. All, however, with the exception of the last named, undergo decussation in the spinal cord, and along it are transmitted to the brain by the grey matter.

d. The posterior columns of the cord appear to have a great share in reflex movements.

e. Impulses of the will, leading to voluntary contractions of muscles, appear to be transmitted principally along the antero-lateral columns, and the contiguous grey matter of the cord.

f. Decussation of motor impulses occurs, not in the spinal cord, as is the case with sensitive impressions, but, as hitherto admitted, at the anterior part of the medulla oblongata (fig. 234). This decussation, however, does not take place, as generally supposed, all along the median line, at the base of the encephalon, but only at that portion of the anterior pyramids which is continuous with the lateral columns of the cord. Hence, the mandates of the will, having made their decussation, first enter the cord by the lateral tracts and adjoining grey matter, and

then pass to the anterior columns and to the grey matter associated with them. Accordingly, division of the anterior pyramids, at the point of decussation (2, fig. 234), is followed by paralysis of motion in all parts below; while division of the olivary bodies, which constitute the true continuations of the anterior columns of the cord, appears to produce very little paralysis. Disease or division of any part of the cerebro-spinal axis *above* the seat of decussation (1, fig. 234) is followed, as well-known, by impaired or lost power of motion on the *opposite* side of the body; while a like injury inflicted *below* this part (3, fig. 234), induces similar paralysis on the *corresponding* side.

Hyperæsthesia, or exalted sensibility, is the constant result of injuries to the posterior columns (Brown-Séquard). When one half of the spinal cord is cut through, complete anæsthesia of the other side of the body below the point of section results, but there is often greatly increased sensibility on the same side; so much so that the least touch appears to be agonising. This condition may persist for several days. Similar effects may, in man, be the result of injury. Thus, in a patient who had sustained a severe lesion of the spinal cord in the cervical region, causing extensive paralysis and loss of sensation in the lower half of the body, there were two circumscribed areas, one on each arm, symmetrically placed, in which the gentlest touch caused extreme pain.

In addition to the transmission of ordinary sensory and motor impulses, the spinal cord is the medium of conduction also of impulses to and from the *vaso-motor centre* in the medulla oblongata.

2. The spinal cord, as a nerve-centre, or rather as an aggregate of many nervous centres, has the power of *transference* and *reflexion* of nervous impulses (p. 497 and 498).

Examples of the *transference* of impressions in the cord have been given (p. 497); and that the transference takes place in the cord, and not in the brain, is nearly proved by the frequent cases of pain felt in the knee and not in the hip, in diseases of the hip; of pain felt in the urethra or glans penis, and not in the bladder, in calculus; for, if both the primary and the

secondary or transferred impression were in the brain, both should be felt.

3. *Reflex Action of Spinal Cord.*—In man and other mammalia the spinal cord is so much under the control of the higher nerve-centres, that its own individual functions in relation to reflex action are apt to be overlooked; and the result of injury, by which the cord is cut off completely from the influence of the encephalon, is apt to lessen rather than increase our notions of its importance and individual endowments. Thus, when the human spinal cord is divided, the lower extremities fall into any position that their weight and the resistance of surrounding objects combine to give them; if the body is irritated, they do not move towards the irritation; and if they are touched, the consequent reflex movements are disorderly and purposeless; all power of voluntary movement is absolutely abolished. In the case of the frog, however, and many other cold-blooded animals, in which experimental and other injuries of the nerve-tissues are better borne, and in which the lower nerve-centres are less subordinate in their action to the higher, the proper reflex functions of the cord are very clearly shown. When, for example, a frog's head is cut off, the limbs remain in, or assume a natural position; they resume it when disturbed; and when the abdomen or back is irritated, the feet are moved with the manifest purpose of pushing away the irritation. It is as if the mind of the animal were still engaged in the acts; and yet all analogy would lead us to the belief that the spinal cord of the frog has no different endowment, in *kind*, from those which belong to the cord of the higher vertebrata; the difference is only in *degree*. And if this be granted, it may be assumed that, in man and the higher animals, many actions are performed as reflex movements occurring through and by means of the spinal cord, although the latter cannot by itself initiate or even direct them independently.

The evident adaptation and purpose in the movements of the cold-blooded animals, have led some to think that they must be conscious and capable of will without their brains. But purposive movements are no proof of consciousness or will in the creature manifesting them. The movements of the limbs of headless frogs are not more purposive than the movements of our

own respiratory muscles are; in which we know that neither will nor consciousness is at all times concerned. It may not, indeed, be assumed that the acts of standing, leaping, and other movements, which decapitated cold-blooded animals can perform, are also always, in the entire and healthy state, performed involuntarily, and under the sole influence of the cord; but it is probable that such acts may be, and commonly are, so performed, the higher nerve-centres of the animal having only the same kind of influence in modifying and directing them, that those of man have in modifying and directing the movements of the respiratory muscles.

The fact that such movements as are produced by irritating the skin of the lower extremities in the human subject, after division or disorganisation of a part of the spinal cord, do not follow the same irritation when the mind is active and connected with the cord through the brain, is, probably, due to the mind ordinarily perceiving the irritation and instantly controlling the muscles of the irritated and other parts; for, even when the cord is perfect, such involuntary movements will often follow irritation, if it be applied when the mind is wholly occupied. When, for example, one is anxiously thinking, even slight stimuli will produce involuntary and reflex movements. So, also, during sleep, such reflex movements may be observed when the skin is touched or tickled; for example, when one touches with the finger the palm of the hand of a sleeping child, the finger is grasped—the impression on the skin of the palm producing a reflex movement of the muscles which close the hand. But when the child is awake, no such effect is produced by a similar touch.

On the whole, it may, from these and like facts, be concluded that reflex acts, performed under the influence of the reflecting power of the spinal cord, are essentially independent of the brain, and may be performed perfectly when the brain is separated from the cord: that these include a much larger number of the natural and purposive movements of the lower animals than of the warm-blooded animals and man: and that over nearly all of them the mind may exercise, through the brain, some control; determining, directing, hindering, or modifying them, either by direct action, or by its power over associated muscles.

As instances in which the spinal cord, by reflex action, determines the combination of muscles, may be mentioned the acts

of the abdominal muscles in vomiting and voiding the contents of the bladder and rectum; in both of which, though, after the period of infancy, the mind may have the power of postponing or modifying the act, there are all the evidences of reflex action; namely, the necessary precedence of a stimulus, the independence of the will, and, sometimes, of consciousness, the combination of many muscles, the perfection of the act without the help of education or experience, and its failure or imperfection in disease of the lower part of the cord. The emission of semen is equally a reflex act governed by the spinal cord: the irritation of the glans penis conducted to the spinal cord, and thence reflected, excites the successive and co-ordinate contractions of the muscular fibres of the vasa deferentia and vesiculæ seminales, and of the accelerator urinæ and other muscles of the urethra; and a forcible expulsion of semen takes place, over which the mind has little or no control, and which, in cases of paraplegia, may be unfelt. The erection of the penis, also, as already explained (p. 216), appears to be in part the result of a reflex contraction of the muscles by which the veins returning the blood from the penis are compressed. The involuntary action of the uterus in expelling its contents during parturition, is also of a purely reflex kind, dependent in part upon the spinal cord, though in part also upon the sympathetic system: its independence of the brain being proved by cases of delivery in paraplegic women, and now more abundantly shown in the use of chloroform.

To these instances of spinal reflex action, some add yet many more, including nearly all the acts which seem to be performed unconsciously, such as those of walking, running, writing, and the like: for these are really involuntary acts. It is true that at their first performances they are voluntary, that they require education for their perfection, and are at all times so constantly performed in obedience to a mandate of the will, that it is difficult to believe in their essentially involuntary nature. But the will really has only a *controlling* power over their performance; it can hasten or stay them, but it has little or nothing to do with the actual carrying out of the effect. And this is proved by the circumstance that these acts can be performed with complete mental abstraction: and, more than this, that the endeavour to carry them out entirely by the exercise of the will is not only not beneficial, but positively interferes with their harmonious and perfect performance. Anyone may convince himself of this fact by trying to take each step as a voluntary act in walking down stairs, or to form each letter or word in writing by a distinct exercise of the will.

These actions, however, will be again referred to, when treating of their possible connection with the functions of the so-called *sensory ganglia*, p. 530.

The phenomena of spinal reflex actions in man are much more striking and unmixed in cases of disease. In some of these, the effect of a morbid irritation, or a morbid irritability of the cord, is very simple; as when the local irritation of sensory fibres, being propagated to the spinal cord, excites merely local spasms, —spasms, namely, of those muscles, the motor fibres of which arise from the same part of the spinal cord as the sensory fibres that are irritated. Of such a case we have instances in the involuntary spasmodic contraction of muscles in the immediate neighbourhood of inflamed joints; and numerous other examples of a like kind might be quoted.

In other instances, in which we must assume that the cord is morbidly more irritable, *i.e.*, apt to issue more nervous force than is proportionate to the stimulus applied to it, a slight impression on a sensory nerve produces extensive reflex movements. This appears to be the condition in tetanus, in which a slight touch on the skin may throw the whole body into convulsion. A similar state is induced by the introduction of strychnia, and, in frogs, of opium, into the blood; and numerous experiments on frogs thus made tetanic, have shown that the tetanus is wholly unconnected with the brain, and depends on the state induced in the spinal cord.

Many reflex actions are capable of being more or less controlled or even altogether prevented by the will: thus an *inhibitory* action may be exercised by the brain over reflex functions of the cord and the other nerve centres.

The following may be quoted as familiar examples of this inhibitory action:—

To prevent the reflex action of crying out when in pain, it is often sufficient firmly to clench the teeth or to grasp some object and hold it tight. When the feet are tickled we can, by an effort of will, prevent the reflex action of jerking them up. So, too, the involuntary closing of the eyes and starting, when a blow is aimed at the head, can be similarly restrained.

Mr. Darwin has mentioned an interesting example of the way in which, on the other hand, such an instinctive reflex act may override the strongest effort of the will. He placed his face close against the glass of the cobra's

cage in the Reptile House at the Zoological Gardens, and though, of course, thoroughly convinced of his perfect security, could not by any effort of the will prevent himself from starting back when the snake struck in fury at the glass.

It may seem to have been implied that the spinal cord, as a single nerve-centre, reflects alike from all parts all the impressions conducted to it. But it is more probable that it should be regarded as a collection of nervous centres united in a continuous column. This is made probable by the fact that segments of the cord may act as distinct nerve-centres, and excite motions in the parts supplied with nerves given off from them; as well as by the analogy of certain cases in which the muscular movements of single organs are under the control of certain circumscribed portions of the cord. Thus,—for the governance of the sphincter-muscles concerned in guarding the orifices respectively of the rectum and urinary bladder, there are special nerve-centres in the lower part of the spinal cord (*ano-spinal* and *vesico-spinal* centres); while the actions of these are temporarily *inhibited* by stimuli which lead to defæcation and micturition. So also, there is a centre directly concerned in erection of the penis and emissio seminis (*genito-urinary*). But these and all other spinal nerve-centres are intimately connected both structurally and physiologically, one with another, as well as with those higher encephalic centres, without whose guiding influence their actions may become disorderly and purposeless, or altogether abrogated.

Volkmann has shown that the rhythmical movements of the anterior pair of lymphatic hearts in the frog depend upon nervous influence derived from the portion of spinal cord corresponding to the third vertebra, and those of the posterior pair on influence supplied by the portion of cord opposite the eighth vertebra. The movements of the heart continue, though the whole of the cord, except the above portions, be destroyed; but on the instant of destroying either of these portions, though all the rest of the cord be untouched, the movements of the corresponding hearts cease. What appears to be thus proved in regard to two portions of the cord, may be inferred to prevail in other portions also; and the inference is reconcilable with most of the facts known concerning the physiology and comparative anatomy of the cord.

The influence of the spinal cord on the sphincter ani has been already mentioned (see above). It maintains this muscle in permanent contraction, so that, except in the act of defæcation,

the orifice of the anus is always closed. This influence of the cord resembles its common reflex action in being involuntary, although the will can act on the muscle to make it contract more, or may inhibit the action of the ano-spinal centre so as to permit its dilatation. The condition of the sphincter ani, however, is not altogether exceptional. It is the same in kind, though it exceeds in degree that condition of muscles which has been called *tone*, or passive contraction ; a state in which they always when not active appear to be during health, and in which, though called inactive, they are in slight contraction, and certainly are not relaxed, as they are long after death, or when the spinal cord is destroyed. This tone of all the muscles of the trunk and limbs depends on the spinal cord, as the contraction of the sphincter ani does. If an animal be killed by injury or removal of the brain, the tone of the muscles may be felt and the limbs feel firm as during sleep ; but if the spinal cord be destroyed, the sphincter ani relaxes, and all the muscles feel loose, and flabby, and atonic, and remain so till *rigor mortis* commences.

This kind of tone must be distinguished from that mere firmness and tension which it is customary to ascribe, under the name of *tone*, to all tissues that feel robust and not flabby, as well as to muscles. The tone peculiar to muscles has in it a degree of vital contraction : that of other tissues is only due to their being well nourished, and therefore compact and tense.

It will have been gathered from the preceding account, that the spinal cord has no power of *automatic* (independent) action, either voluntary or involuntary. Its power as a nerve-centre over and beyond that of *conduction* is confined to the *transference* and *reflection* of impressions which are conveyed to it from other parts of the body.

THE MEDULLA OBLONGATA.

The medulla oblongata (figs. 235, 236) is a column of grey and white nervous substance formed by the prolongation upwards of the spinal cord and connecting it with the brain. The grey substance which it contains is situated in the interior, and variously divided into masses and laminæ by the white or fibrous

substance which is arranged partly in external columns, and partly in fasciculi traversing the central grey matter. The medulla oblongata is larger than any part of the spinal cord. Its columns are pyriform, enlarging as they proceed towards the brain, and are continuous with those of the spinal cord.

Fig. 235.*

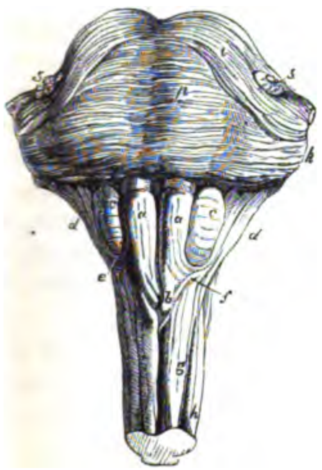
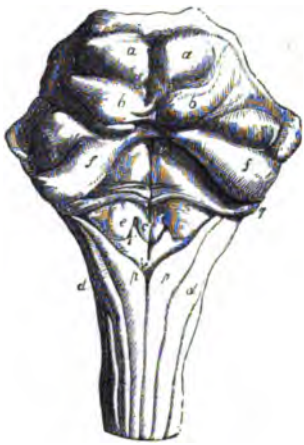


Fig. 236.†



Each half of the medulla, therefore, may be divided into three columns or tracts of fibres, continuous with the three tracts of which each half of the spinal cord is made up. The columns are more prominent than those of the spinal cord, and separated

* Fig. 235. View of the anterior surface of the pons Varolii, and medulla oblongata. *a, a,* anterior pyramids. *b,* their decussation; *c, c,* olivary bodies; *d, d,* restiform bodies; *e,* arciform fibres; *f,* fibres described by Solly as passing from the anterior column of the cord to the cerebellum; *g,* anterior column of the spinal cord; *h,* lateral column; *p,* pons Varolii; *i,* its upper fibres; 5, 5, roots of the fifth pair of nerves.

† Fig. 236. View of the posterior surface of the pons Varolii, corpora quadrigemina, and medulla oblongata. The peduncles of the cerebellum are cut short at the side. *a, a,* the upper pair of corpora quadrigemina; *b, b,* the lower; *f, f,* superior peduncles of the cerebellum; *c,* eminence connected with the nucleus of the hypoglossal nerve; *e,* that of the glosso-pharyngeal nerve; *i,* that of the vagus nerve; *d, d,* restiform bodies; *p, p,* posterior pyramids; *v, v,* groove in the middle of the fourth ventricle, ending below in the calamus scriptorius; 7, 7, roots of the auditory nerves.

from each other by deeper grooves. The *anterior*, continuous with the anterior columns of the cord, are called the anterior *pyramids*; the *posterior*, continuous with the posterior columns of the cord, are called the *restiform* bodies; and the *lateral*, continuous with the lateral columns of the cord, are named simply from their position. On the fibres of the lateral column of each side, near its upper part, is a small oval mass containing grey matter, and named the *olivary body*; and at the posterior part of the restiform column, immediately on each side of the posterior median groove, a small tract is marked off by a slight groove from the remainder of the restiform body, and called the *posterior pyramid*. The restiform columns, instead of remaining parallel with each other throughout the whole of the medulla oblongata, diverge near its upper part, and by thus diverging, lay open, so to speak, a space called the fourth ventricle, the floor of which is formed by the grey matter of the interior of the medulla, by this divergence exposed.

On separating the anterior pyramids, and looking into the groove between them, some decussating fibres can be plainly seen.

Distribution of the Fibres of the Medulla Oblongata.

The *anterior pyramid* of each side, although mainly composed of continuations of the fibres of the anterior columns of the spinal cord, receives fibres from the lateral columns, both of its own and the opposite side; the latter fibres forming almost entirely those decussating strands before mentioned, which are seen in the groove between the anterior pyramids.

Thus composed, the anterior pyramidal fibres proceeding onwards to the brain are distributed in the following manner:—1. The greater part pass on through the pons to the cerebrum. A portion of the fibres, however, running apart from the others, joins some fibres from the olivary body, and unites with them to form what is called the *olivary fasciculus* or *fillet*. 2. A small tract of fibres proceeds to the cerebellum.

The *lateral column* on each side of the medulla, in proceeding upwards, divides into three parts, outer, inner, and middle, which are thus disposed of:—1. The *outer* fibres go with the restiform tract to the cerebellum. 2. The *middle* decussate across the middle line with their fellows, and form a part of the anterior pyramid of the opposite side. 3. The *inner* pass on to the cerebrum along the floor of the fourth ventricle, on each side, under the name of the *fasciculus teres*.

The fibres of the *restiform* body receive some small contributions, as before mentioned, from both the lateral and anterior columns of the medulla, and proceed chiefly to the cerebellum, but that small part behind, called *posterior*

pyramid, is continued on with the fasciculus teres of each side along the floor of the fourth ventricle to the cerebrum.

The expressions "continuous fibres," and the like, appear to be usually understood as meaning that certain primitive nerve-fibres pass without interruption from one part to another. But such continuity of primitive fibres through long distances in the nervous centres is very far from proved. The apparent continuity of fasciculi (which is all that dissection can yet trace) is explicable on the supposition that many comparatively short fibres lie parallel, with the ends of each inlaid among many others. In such a case, there would be an apparent continuity of fibres; just as there is, for example, when one untwists and picks out a long cord of silk or wool, in which each fibre is short, and yet each fasciculus appears to be continued through the whole cord.

Functions of the Medulla Oblongata.

The functions of the medulla oblongata, like those of the spinal cord, may be considered under the heads of: 1. Conduction; 2. Transference and Reflexion; and, in addition, though somewhat doubtfully; 3. Automatism.

1. In *conducting* impressions the medulla oblongata has a wider extent of function than any other part of the nervous system, since it is obvious that all impressions passing to and fro between the brain and the spinal cord and all nerves arising below the pons, must be transmitted through it.

The decussation of part of the fibres of the anterior pyramids of the medulla oblongata (p. 522), explains the phenomena of cross-paralysis, as it is termed, *i.e.*, of the loss of *motion* in cerebral apoplexy being always on the side opposite to that on which the effusion of blood has taken place. Looking only to the anatomy of the medulla oblongata, it was not possible to explain why the loss of *sensation* also is on the side opposite the injury or disease of the brain: for there is no evidence of a decussation of posterior fibres like that which ensues among the fibres of the anterior pyramids of the medulla oblongata. But Brown-Séquard has shown that the crossing of sensory impressions occurs in the spinal cord (p. 513).

2. As a nerve-centre by which impressions are *transferred* or *reflected*, the medulla oblongata also resembles the spinal cord; the only difference between them consisting of the fact that many of the reflex actions performed by the former are much more important to life than any performed by the spinal cord; and one of its reflex actions at least—that of respiration, is essential, in the higher Vertebrata, to the continuance of life for even a few moments.

It has been proved by repeated experiments on the lower animals that the entire brain may be gradually cut away in successive portions, and yet life may continue for a considerable time, and the respiratory movements be uninterrupted. Life may also continue when the spinal cord is cut away in successive portions from below upwards as high as the point of origin of the phrenic nerve. In Amphibia, these two experiments have been combined: the brain being all removed from above, and the cord from below; and so long as the medulla oblongata was intact, respiration and life were maintained. But if, in any animal, the medulla oblongata is wounded, particularly if it is wounded in its central part, opposite the origin of the pneumogastric nerves, the respiratory movements cease, and the animal dies as if asphyxiated. And this effect ensues even when all parts of the nervous system, except the medulla oblongata, are left intact.

Injury and disease in men prove the same as these experiments on animals. Numerous instances are recorded in which injury to the human medulla oblongata has produced instantaneous death; and, indeed, it is through injury of it, or of the part of the cord connecting it with the origin of the phrenic nerve, that death is commonly produced in fractures and diseases with sudden displacement of the upper cervical vertebræ.

The centre whence the nervous force for the production of combined respiratory movements appears to issue is in the interior of that part of the medulla oblongata from which the pneumogastric nerves arise. The pneumogastric nerves themselves, indeed, are not essential to the respiratory movements; for both may be divided without more immediate effect than a retardation of these movements. But this part of the medulla oblongata is the nerve-centre whereby the impulses producing the respiratory movements are *reflected* (p. 258).

The wide extent of connection which belongs to the medulla oblongata as the centre of the respiratory movements, is shown by the fact that impressions by mechanical and other ordinary stimuli, made on many parts of the external or internal surface of the body, may induce respiratory movements. Thus involuntary respirations are induced by the sudden contact of cold with any part of the skin, as in dashing cold water into the face. Irritation of the mucous membrane of the nose produces sneezing. Irritation in the pharynx, œsophagus, stomach, or intestines, excites the concurrence of the respiratory movements to produce vomiting. Violent irritation in the rectum, bladder, or uterus, gives rise to a concurrent action of the respiratory muscles, so as to effect the expulsion of the fæces, urine, or fœtus.

It would appear that much of the reflecting power of the medulla oblongata may be destroyed, and yet its power in the respiratory movements may remain. Thus, in patients completely under the influence of chloroform, the winking of the eye-lids ceases, and irritation of the pharynx will not produce the usual movements of swallowing, or the closure of the glottis (so that blood may run quietly into the stomach, or even into the lungs); yet, with all this, they may breathe steadily, and show that the power of the medulla oblongata to combine in action all the nerves of the respiratory muscles is perfect.

The medulla oblongata appears to be the centre whence are derived the motor impulses enabling the muscles of the palate, pharynx, and œsophagus, to produce the successive co-ordinate and adapted movements necessary to the act of *deglutition* (p. 295). This is proved by the persistence of swallowing in some of the lower animals after destruction of the cerebral hemispheres and cerebellum; its existence in anencephalous monsters; the power of swallowing possessed by marsupial embryoes before the brain is developed; and by the complete arrest of the power of swallowing when the medulla oblongata is injured in experiments.

The medulla oblongata contains several other nerve-centres than those concerned with (1) respiration, (2) deglutition. The following are those, the presence of which has been best established: (3) A centre by which the movements of mastication are regulated (p. 284). (4) Through the medulla oblongata, chiefly, are reflected the impressions which excite the secretion of saliva (p. 288). (5) Centre for the regulation of the action of the heart, through the pneumogastrics and probably, also, for the accelerating fibres of the sympathetic (p. 167). (6) The chief *vasomotor* centre. From this centre arise fibres which, passing down the spinal cord, issue with the anterior roots of the spinal nerves, and enter the ganglia and branches of the sympathetic system, by which they are conducted to the blood-vessels (p. 188). (7) Cilio-spinal centre for the regulation of the iris, and other plain-fibred muscles of the eye. (8 and 9) Centres or ganglia of the special senses of hearing and taste. (10) The centre for speech, *i.e.*, the centre by which the various muscular movements concerned in speech are co-ordinated or harmonised.

The so-called *diabetic* centre, or, in other words, the grey

matter in the medulla oblongata which, being irritated, causes glycosuria (p. 360), is probably the vasomotor centre; and this peculiar result of its stimulation is merely due to vasomotor changes in the liver.

Though respiration and life continue while the medulla oblongata is perfect and in connection with the respiratory nerves, yet, when all the brain above it is removed, there is no more appearance of sensation, or will, or of any mental act in the animal, the subject of the experiment, than there is when only the spinal cord is left. The movements are all involuntary and unfelt; and the medulla oblongata has, therefore, no claim to be considered as an organ of the mind, or as the seat of sensation or voluntary power. These are connected with parts to be afterwards described.

STRUCTURE AND PHYSIOLOGY OF THE PONS VAROLII, CRURA CEREBRI, CORPORA QUADRIGEMINA, CORPORA GENICULATA, OPTIC THALAMI, AND CORPORA STRIATA.

Pons Varolii.—The meso-cephalon, or pons (VI, fig. 237), is composed principally of transverse fibres connecting the two hemispheres of the cerebellum, and forming its principal transverse commissure. But it includes, interlacing with these, numerous longitudinal fibres which connect the medulla oblongata with the cerebrum, and transverse fibres which connect it with the cerebellum. Among the fasciculi of nerve-fibres by which these several parts are connected, the pons also contains abundant grey or vesicular substance, which appears irregularly placed among the fibres, and fills up all the interstices.

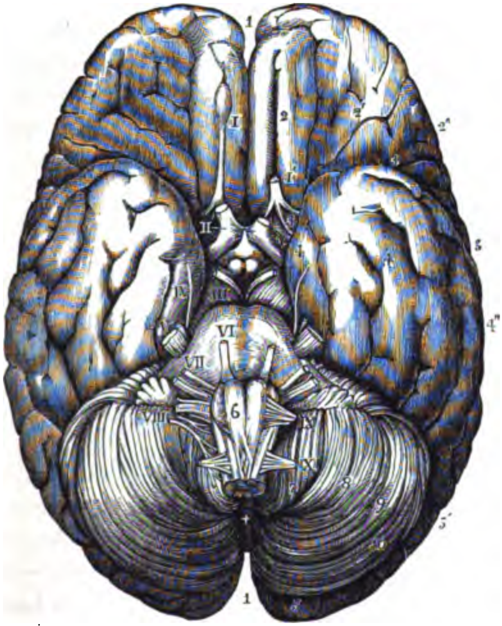
The anatomical distribution of the fibres, both transverse and longitudinal, of which the pons is composed, is sufficient evidence of its functions as a conductor of impressions from one part of the cerebro-spinal axis to another.

Concerning its functions as a nerve-centre, little or nothing is certainly known.

Crura Cerebri.—The *crura cerebri* (III, fig. 237), are principally formed of nerve-fibres, of which the inferior or more superficial are continuous with those of the anterior pyramidal

tracts of the medulla oblongata, and the superior or deeper fibres with the lateral and posterior pyramidal tracts, and with the olivary fasciculus. Besides these fibres from the medulla oblongata, are others from the cerebellum; and some of the

Fig. 237.*



latter as well as a part of the fibres derived from the lateral tract of the medulla oblongata, decussate across the middle line.

On their upper part, the crura cerebri bear three pairs of small ganglia, or masses of mingled grey and white nerve-substance, namely, the *corpora geniculata externa* and *interna*, and

* Fig. 237. Base of the brain.—1, superior longitudinal fissure; 2, 2', 2", anterior cerebral lobe; 3, fissure of Sylvius, between anterior and 4, 4', 4", middle cerebral lobe; 5, 5', posterior lobe; 6, medulla oblongata; the figure is in the right anterior pyramid; 7, 8, 9, 10, the cerebellum; +, the inferior vermiform process. The figures from I. to IX. are placed against the corresponding cerebral nerves; III. is placed on the right crus cerebri; VI. and VII. on the pons Varolii; X. the first cervical or suboccipital nerve. (Allen Thomson.) ½.

the *corpora quadrigemina.* And in their onward course to the cerebrum, the fibres of each crus cerebri pass through two large ganglia on each side the *optic thalamus* and *corpus striatum*, and in their substance come into connection with variously-shaped masses and layers of grey substance. Whether all the fibres of the crura cerebri end in the grey matter of these two ganglia, while others start afresh from them to enter the cerebral hemispheres; or whether some of the fibres of the crura pass through them, while only a portion can be strictly said to have their termination there, must remain at present undecided; the difficulties in the way of solving such an anatomical doubt being at present insuperable.

Each crus cerebri contains among its fibres a mass of grey substance, the *locus niger.*

With regard to their functions, the crura cerebri may be regarded as, principally, conducting organs. As nerve-centres they are probably connected with the functions of the third cerebral nerve, which arises from the *locus niger*, and through which are directed the chief of the numerous and complicated movements of the eyeball.

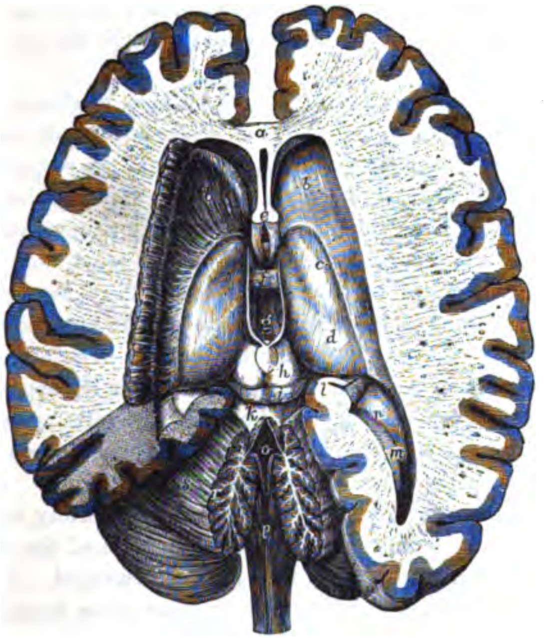
Corpora Quadrigemina.—The corpora quadrigemina (from which, in function, the *corpora geniculata* are not distinguishable), are the homologues of the optic lobes in Birds, Amphibia and Fishes, and may be regarded as the principal nerve-centres for the sense of sight. The experiments of Flourens, Longet, and Hertwig, show that removal of the corpora quadrigemina wholly destroys the power of seeing; and diseases in which they are disorganised are usually accompanied with blindness. Atrophy of them is also often a consequence of atrophy of the eyes.

Destruction of one of the corpora quadrigemina (or of one optic lobe in birds), produces blindness of the opposite eye.

This loss of sight is the only apparent injury of sensibility sustained by the removal of the corpora quadrigemina. The removal of one of them affects the movements of the body, so that animals rotate, as after division of the crus cerebri, only more slowly: but this is probably due to giddiness and partial loss of sight. The more evident and direct influence is that pro-

duced on the iris. It contracts when the corpora quadrigemina

Fig. 238.*



* Fig. 238. Dissection of brain, from above, exposing the lateral, fourth, and fifth ventricles, with the surrounding parts (from Hirschfeld and Leveillé). ½.—*a*, anterior part, or *genu* of corpus callosum; *b*, corpus striatum; *b'*, the corpus striatum of left side, dissected so as to expose its grey substance; *c*, points by a line to the tænia semicircularis; *d*, optic thalamus; *e*, anterior pillars of fornix divided; below they are seen descending in front of the third ventricle, and between them is seen part of the anterior commissure; in front of the letter *e* is seen the slit-like fifth ventricle, between the two laminæ of the septum lucidum; *f*, soft or middle commissure; *g* is placed in the posterior part of the third ventricle; immediately behind the latter are the posterior commissure (just visible) and the pineal gland, the two crura of which extend forwards along the inner and upper margins of the optic thalami; *h* and *i*, the corpora quadrigemina; *k*, superior crus of cerebellum; close to *k* is the valve of Vieussens, which has been divided so as to expose the fourth ventricle; *l*, hippocampus major and corpus fimbriatum, or tænia hippocampi; *m*, hippocampus minor; *n*, eminentia collateralis; *o*, fourth ventricle; *p*, posterior surface of medulla oblongata; *r*, section of cerebellum; *s*, upper part of left hemisphere of cerebellum exposed by the removal of part of the posterior cerebral lobe.

are irritated: it is always dilated when they are removed: so that they may be regarded, in some measure at least, as the nervous centres governing its movements, and adapting them to the impressions derived from the retina through the optic nerves and tracts.

Concerning the functions, taken as a whole, discharged by the olfactory and optic lobes, and the other centres of nerves of special sense, the grey substance of the pons, the corpora striata and optic thalami (*b*, *d*, fig. 238), the most philosophical theory is undoubtedly that which has been so ably enunciated by Dr. Carpenter. He supposes these ganglia to constitute the real sensorium; that is to say, it is by means of them that the mind becomes conscious of impressions made on the organs or tissues with which (by means of nerve-fibres) they are in communication. Thus impressions made on the optic nerve, or its expansion in the retina, are conducted by the fibres of the optic nerve to the corpora quadrigemina, and through the medium of these ganglia the mind becomes conscious of the impression made. And impressions on the filaments of the olfactory or auditory nerve are in the same way perceived through the medium of the olfactory or auditory ganglia, to which they are first conveyed. The optic thalami and corpora striata probably have some function of a like kind—perhaps in relation to ordinary sensation, but nothing is certainly known regarding them.

Besides their functions, however, as media of communication between the mind and external objects, these *Sensory Ganglia*, as they are termed, are probably the nerve-centres by means of which those reflex acts are performed which require either a higher combination of muscular acts than can be directed by means of the medulla oblongata or spinal cord *alone*, or on the other hand, such reflex actions as require for their right performance the guidance of sensation. Under this head are included various acts, as walking, reading, writing, and the like, which we are accustomed to consider voluntary, but which really are as incapable of being performed by distinct and definite acts of the will as are those more simple movements of which we are not conscious, and which, performed under the guidance of the spinal

cord or medulla oblongata alone, we call simple reflex actions. It is true that in the performance of such acts as those just mentioned, a certain exercise of the will is required at the commencement, but that the carrying out of its mandates is essentially reflex and involuntary, anyone may convince himself by trying to perform each individual movement concerned, strictly as a voluntary act (p. 517).

That such movements are reflex and essentially independent —at least, in their habitual performance—of the will, there is no doubt: that the nerve-centres through which such reflex actions are performed are, in addition to the medulla oblongata and spinal cord, the so-called Sensory Ganglia, is, of course, only a theory which may or may not be confirmed by future investigations.

Besides their possible functions in the manner just-mentioned, it is supposed that the sensory ganglia may be the medium of transmission of impulses of the will (Cerebrum) to the muscles which act in obedience to it, and thus be the centres of reflex action as well for impressions conveyed *downwards* to them from the Cerebral hemispheres, as for impressions carried *upwards* to them by the different nerves which preserve their connection with the organs of the various senses.

THE CEREBELLUM.

The Cerebellum (7, 8, 9, 10, fig. 237) is composed of an elongated central portion called the vermiform processes, and two hemispheres. Each hemisphere is connected with its fellow, not only by means of the vermiform processes, but also by a bundle of fibres called the *middle crus* or *peduncle* (the latter forming the greater part of the pons Varolii), while the *superior crura* with the valve of Vieussens, connect it with the cerebrum (fig. 239, 5), and the *inferior crura* (formed by the prolonged restiform bodies) connect it with the medulla oblongata (3, fig. 239).

The cerebellum is composed of white and grey matter, the latter being external, like that of the cerebrum, and, like it, infolded, so that a larger area may be contained in a given

space. The convolutions of the grey matter, however, are arranged after a different pattern as shown in fig. 239.

Fig. 239.*

Besides the grey substance on the surface, there is, near the centre of the white substance of each hemisphere, a small capsule of grey matter called the *corpus dentatum* (fig. 240, *cd*), resembling very closely the *corpus dentatum* of the olivary body of the medulla oblongata (fig. 240, *o*).

If a section be taken through the cortical portion of the cerebellum, the following distinct layers can be seen (fig. 241).

(1) Immediately beneath the pia mater (*p m*) is a layer of considerable thickness, which consists of a delicate connective tissue, in which are scattered several spherical corpuscles like those of the granular layer of the retina, and also an immense number of

* Fig. 239. View of cerebellum in section and of fourth ventricle, with the neighbouring parts (from Sappey after Hirschfeld and Leveillé). 1, median groove of fourth ventricle, ending below in the *calamus scriptorius*, with the longitudinal eminences formed by the *fasciculi teretes*, one on each side; 2, the same groove, at the place where the white streaks of the auditory nerve emerge from it to cross the floor of the ventricle; 3, inferior crus or peduncle of the cerebellum, formed by the restiform body; 4, posterior pyramid; above this is the calamus scriptorius; 5, superior crus of cerebellum, or processus e cerebello ad cerebrum (or ad testes); 6, 6, fillet to the side of the crura cerebri; 7, 7, lateral grooves of the crura cerebri; 8, corpora quadrigemina.

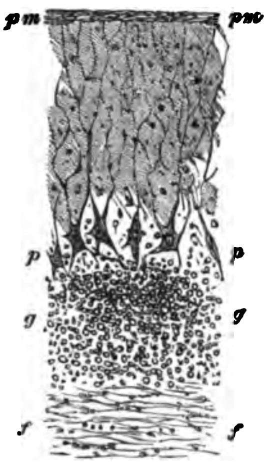
delicate fibres passing up towards the free surface and branching as they go. These fibres are the processes of

(2) *The Cells of Purkinje* (*p*).

These are a single layer of branched nerve-cells, which give off a single unbranched process downwards, and numerous processes up into the external layer, some of which become continuous with the scattered corpuscles.

Fig. 240.*

Fig. 241.†



(3) *The granule layer* (*g*), consisting of immense numbers of corpuscles closely resembling those of the nuclear layers of the retina.

* Fig. 240. Outline sketch of a section of the cerebellum showing the *corpus dentatum.* The section has been carried through the left lateral part of the pons, so as to divide the superior peduncle and pass nearly through the middle of the left cerebellar hemisphere. The olivary body has also been divided longitudinally so as to expose in section its *corpus dentatum.* *c r*, crus cerebri; *f*, fillet; *q*, corpora quadrigemina; *s p*, superior peduncle of the cerebellum divided; *m p*, middle peduncle or lateral part of the pons Varolii, with fibres passing from it into the white stem; *a v*, continuation of the white stem radiating towards the arbor vitæ of the folia; *c d*, corpus dentatum; *o*, olivary body with its corpus dentatum; *p*, anterior pyramid (Allen Thomson). ‡.

† Fig. 241. Vertical section of dog's cerebellum; *p m*, pia mater; *p*, corpuscles of Purkinje, which are branched nerve-cells lying in a single layer and sending single processes downwards and more numerous ones upwards, which branch continuously and extend through the deep "molecular layer" towards the free surface; *g*, dense layer of ganglionic corpuscles, closely resembling nuclear layers of retina; *f*, layer of nerve-fibres, with a few scattered ganglionic corpuscles. This last layer (*f f*) constitutes part of the *white* matter of the Cerebellum, while the layers between it and the free surface are *grey* matter (Schofield).

(4) *Nerve-fibre layer* (*f*). Bundles of nerve-fibres forming the white matter of the cerebellum, which, from its branched appearance, has been named the "arbor vitæ."

Functions of the Cerebellum.

The physiology of the Cerebellum may be considered in its relation to sensation, voluntary motion, and the instincts or higher faculties of the mind. Its functions, like those of every other part of the nervous system, are to be determined by physiological experiment, by pathological observation, and by its comparative anatomy. It is itself insensible to irritation, and may be all cut away without eliciting signs of pain (Longet). Yet, if any of its crura be touched, pain is indicated; and, if the restiform tracts of the medulla oblongata be irritated, the most acute suffering appears to be produced. Its removal or disorganization by disease is also generally unaccompanied by loss or disorder of sensibility; animals from which it is removed can smell, see, hear, and feel pain, to all appearance, as perfectly as before (Flourens; Magendie). So that, although the restiform tracts of the medulla oblongata, which themselves appear so sensitive, enter the cerebellum, it cannot be regarded as a principal organ of sensibility.

In reference to motion, the experiments of Longet and most others agree that no irritation of the cerebellum produces movement of any kind. Remarkable results, however, are produced by removing parts of its substance. Flourens (whose experiments have been confirmed by those of Bouillaud, Longet, and others) extirpated the cerebellum in birds by successive layers. Feebleness and want of harmony of muscular movements were the consequence of removing the superficial layers. When he reached the middle layers, the animals became restless without being convulsed; their movements were violent and irregular, but their sight and hearing were perfect. By the time that the last portion of the organ was cut away, the animals had entirely lost the powers of springing, flying, walking, standing, and preserving their equilibrium. When an animal in this state was laid upon its back, it could not recover its former posture,

but it fluttered its wings, and did not lie in a state of stupor; it saw the blow that threatened it, and endeavoured to avoid it. Volition, sensation, and memory, therefore, were not lost, but merely the faculty of combining the actions of the muscles; and the endeavours of the animal to maintain its balance were like those of a drunken man.

The experiments afforded the same results when repeated on all classes of animals; and, from them and the others before referred to, Flourens inferred that the cerebellum belongs neither to the sensory nor the intellectual apparatus; and that it is not the source of voluntary movements, although it belongs to the motor-apparatus; but is the organ for the co-ordination of the voluntary movements, or for the excitement of the *combined* action of muscles.

Such evidence as can be obtained from cases of disease of this organ confirms the view taken by Flourens; and, on the whole, it gains support from comparative anatomy; animals whose natural movements require most frequent and exact combinations of muscular actions being those whose cerebella are most developed in proportion to the spinal cord.

M. Foville holds that the cerebellum is the organ of *muscular sense*, *i.e.*, the organ by which the mind acquires that knowledge of the actual state and position of the muscles which is essential to the exercise of the will upon them; and it must be admitted that all the facts just referred to are as well explained on this hypothesis as on that of the cerebellum being the organ for combining movements. A harmonious combination of muscular actions must depend as much on the capability of appreciating the condition of the muscles with regard to their tension, and to the force with which they are contracting, as on the power which any special nerve-centre may possess of exciting them to contraction. And it is because the power of such harmonious movement would be equally lost, whether the injury to the cerebellum involved injury to the seat of muscular sense, or to the centre for combining muscular actions, that experiments on the subject afford no proof in one direction more than the other.

Gall was led to believe, that the cerebellum is the organ of physical love, or, as Spurzheim called it, of amativeness; and such is still a popular belief among phrenologists. This view has, however, been abundantly disproved.

In opposition to the above theory, it may be stated that there has been a case of complete disorganization or absence of the cerebellum without loss of sexual passion (Combiette, Longet, and Cruveilhier); that the cocks from whom M. Flourens removed the cerebellum showed sexual desire, though they were incapable of gratifying it; and that among animals there is no proportion observable between the size of the cerebellum and the apparent development of the sexual passion. Among the Amphibia, the sexual passion is apparently very strong in frogs and toads; yet the cerebellum is only a narrow bar of nervous substance. Among birds there is no enlargement of the cerebellum in the males that are polygamous; the domestic cock's cerebellum is not larger than the hen's, though his sexual passion must be estimated at many times greater than hers. Among Mammalia the same rule holds; and in this class the experiments of M. Lassaigne have plainly shown that the abolition of the sexual passion by removal of the testes in early life is not followed by any diminution of the cerebellum; for in mares and stallions the average absolute weight of the cerebellum is 61 grains, and in geldings 70 grains; and its proportionate weight, compared with that of the cerebrum, is, on an average, as 1 : 6·59 in mares; as 1 : 5·97 in geldings, and only as 1 : 7·07 in stallions.

The influence of each half of the cerebellum is directed to muscles on the opposite side of the body; and it would appear that for the right ordering of movements, the actions of its two halves must be always mutually balanced and adjusted. For if one of its crura, or if the pons on either side of the middle line, be divided, so as to cut off from the medulla oblongata and spinal cord the influence of one of the hemispheres of the cerebellum, strangely disordered movements ensue. The animals fall down on the side opposite to that on which the crus cerebelli has been divided, and then roll over continuously and repeatedly; the rotation being always round the long axis of their bodies, and from the side on which the injury has been inflicted. The rotations sometimes take place with much rapidity; as often, according to M. Magendie, as sixty times in a minute, and may last for several days. Similar movements have been observed in men; as by M. Serres in a man in whom there was apoplectic effusion in the right crus cerebelli; and by M. Belhomme in a

woman, in whom an exostosis pressed on the left crus.* They may, perhaps, be explained by assuming that the division or injury of the crus cerebelli produces paralysis or imperfect and disorderly movements of the opposite side of the body; the animal falls, and then, struggling with the disordered side on the ground, and striving to rise with the other, pushes itself over; and so, again and again, with the same act, rotates itself. Such movements cease when the other crus cerebelli is divided; but probably only because the paralysis of the body is thus made almost complete.

THE CEREBRUM.

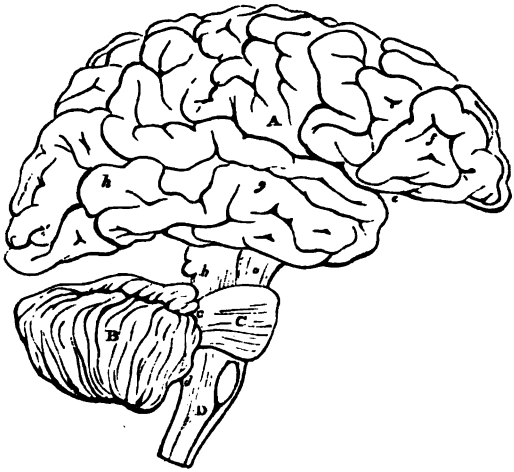
The Cerebrum (composed of two so-called *cerebral hemispheres*) is placed in connection with the pons and medulla oblongata by its two *crura* or *peduncles* (III. fig. 237): it is connected with the cerebellum, by the processes called superior crura of the cerebellum, or *processus a cerebello ad testes*, and by a layer of grey matter, called the valve of Vieussens, which lies between these processes, and extends from the inferior vermiform process of the cerebellum to the corpora quadrigemina of the cerebrum. These parts, which thus connect the cerebrum with the other principal divisions of the cerebro-spinal system, may, therefore, be regarded as the continuation of the cerebro-spinal axis or column; on which, as a kind of offset from the main nerve-path, the cerebellum is placed; and on the further continuation of which, in the direct line, is placed the cerebrum (fig. 242).

The cerebrum is constructed, like the other chief divisions of the cerebro-spinal system, of grey (vesicular and fibrous) and white (fibrous) matter; and, as in the case of the cerebellum (and unlike the spinal cord and medulla oblongata), the grey matter (*cortex*) is external, and forms a capsule or covering for the white substance. For the evident purpose of increasing its amount without undue occupation of space, the grey matter is variously infolded so as to form the cerebral *convolutions*.

* See such cases collected and recorded by Dr. Paget in the Ed. Med. and Surg. Journal for 1847.

Convolutions of the Cerebrum.—For convenience of description, the surface of the brain has been divided into five lobes (Gratiolet).

Fig. 242.*



1. *Frontal* (F. figs. 243, 244), limited behind by the fissure of Rolando (central fissure), and beneath by the fissure of Sylvius.

Its surface consists of three main convolutions, which are approximately horizontal in direction and are broken up into numerous secondary gyri. They are termed the superior, middle, and inferior frontal convolutions. In addition, the frontal lobe contains, at its posterior part, a convolution which runs upwards almost vertically ("ascending frontal"), and is bounded in front by a fissure termed the precentral, behind by that of Rolando.

2. *Parietal* (P.). This lobe is bounded in front by the fissure of Rolando, behind by the external perpendicular fissure (parieto-occipital), and below by the fissure of Sylvius.

Behind the fissure of Rolando is the "ascending parietal" convolution, which swells out at its upper end into what is termed the superior parietal lobule. The superior parietal lobule is separated from the inferior parietal lobule by the intra-parietal sulcus.

The inferior parietal lobule (pli courbe) is situated at the posterior and upper end of the fissure of Sylvius; it consists of (*a*) an anterior part (supramarginal convolution) which hooks round the end of the fissure of Sylvius,

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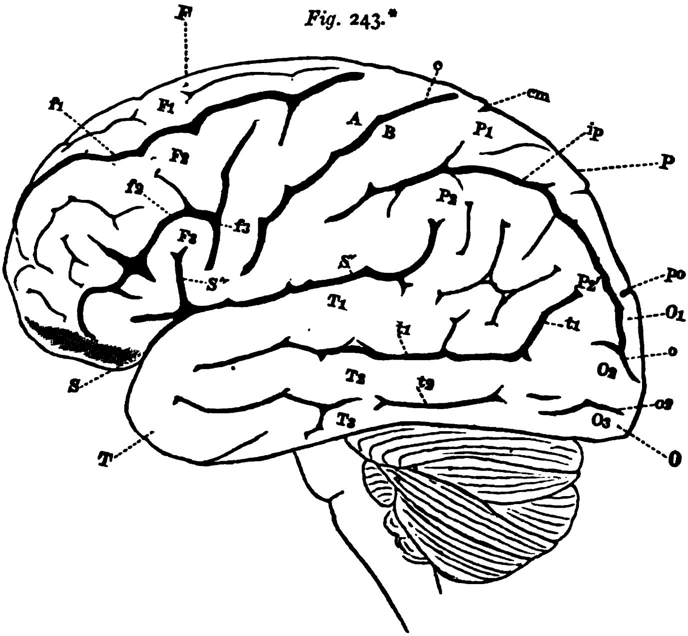
* Fig. 242. Plan in outline of the encephalon, as seen from the right side. ½. (From Quain).—The parts are represented as separated from one another somewhat more than natural, so as to show their connections. A, cerebrum; *f*, *g*, *h*, its anterior, middle, and posterior lobes; *e*, fissure of Sylvius; B, cerebellum; C, pons Varolii; D, medulla oblongata; *a*, peduncles of the cerebrum; *b*, *c*, *d*, superior, middle, and inferior peduncles of the cerebellum.

and joins the superior temporal convolution, and a posterior part (*b*) (angular gyrus) which hooks round into the middle temporal convolution.

3. *Temporo-sphenoidal* (T.), contains three well-marked convolutions,

Fig. 243.*



parallel to each other, termed the superior, middle, and inferior temporal. The superior and middle are separated by the parallel fissure.

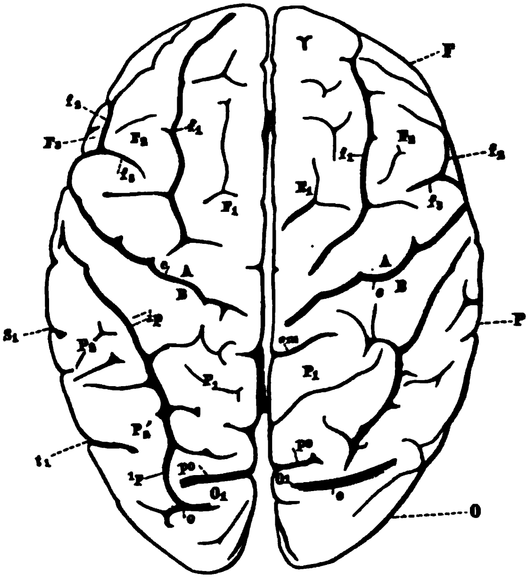
4. *Occipital* (O.). This lobe lies behind the external perpendicular or parieto-occipital fissure, and contains three convolutions, termed the superior, middle, and inferior occipital. They are often not well marked.

* Fig. 243. Lateral view of the brain (semi-diagrammatic). F, Frontal lobe; P, Parietal lobe; O, Occipital lobe; T, Temporo-sphenoidal lobe; S, fissure of Sylvius; S', horizontal, S'', ascending ramus of the same; c, sulcus centralis (fissure of Rolando); A, ascending frontal; B, ascending parietal convolution; F1, superior; F2, middle; F3, inferior frontal convolutions; f1, superior, f2, inferior frontal sulcus; f3, præcentral sulcus; P1, superior parietal lobule; P2, inferior parietal lobule consisting of P2, supramarginal gyrus, and P2', angular gyrus; ip, interparietal sulcus; cm, termination of calloso-marginal fissure; O1, first; O2, second; O3, third occipital convolutions; po, parieto-occipital fissure; o, transverse occipital fissure; o2, sulcus occipitalis inferior; T1, first; T2, second; T3, third temporo-sphenoidal convolutions; t1, first; t2, second temporo-sphenoidal fissures (Ecker).

In man, the external parieto-occipital fissure is only to be distinguished as a notch in the inner edge of the hemisphere; below this it is quite obliterated by the four annectent gyri (plis de passage) which run nearly horizontally.

The upper two connect the parietal, and the lower two the temporal with the occipital lobe.

Fig. 244.*



5. The *central lobe*, or island of Reil, which contains a number of radiating convolutions (gyri operti).

The *internal* surface (Fig. 245) contains the following gyri and sulci:

Gyrus fornicatus, a long curved convolution, parallel to and curving round the corpus collosum, and swelling out at its hinder and upper end into the quadrate lobule (præcuneus), which is continuous with the superior parietal lobule on the external surface.

Marginal convolution runs parallel to the preceding, and occupies the space between it and the edge of the longitudinal fissure.

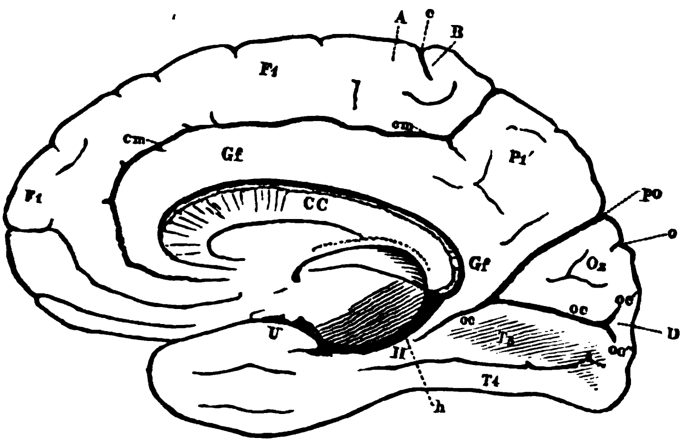
The two convolutions are separated by the calloso-marginal fissure.

The *internal perpendicular* fissure is well marked, and runs downwards to its junction with the *calcarine* fissure: the wedge-shaped mass intervening

* Fig. 244. View of the brain from above (semi-diagrammatic). S1, end of horizontal ramus of fissure of Sylvius. The other letters refer to the same parts as in Fig. 243 (Ecker).

between these two is termed the *cuneus*. The calcarine fissure corresponds to the projection into the posterior cornu of the lateral ventricle, termed the *Hippocampus minor*.

Fig. 245.*



The *temporo-sphenoidal lobe* on its internal aspect is seen to end in a hook (uncinate gyrus). The notch round which it curves is continued up and back as the dentate or hippocampal sulcus: this fissure underlies the projection of the hippocampus major within the brain. There are three internal temporo-occipital convolutions, of which the superior and inferior ones are usually well marked, the middle one generally less so.

The collateral fissure (corresponding to the eminentia collateralis) forms the lower boundary of the superior temporo-occipital convolution.

All the above details will be found indicated in the diagrams (figs. 243, 244, 245).

Structure of the Cerebrum.

The cortical grey matter of the brain consists of three layers of grey matter, alternating with three of a paler tint—white matter; the most external layer consisting of white matter.

* Fig. 245. View of the right hemisphere in the median aspect (semi-diagrammatic). CC, corpus callosum longitudinally divided; Gf, gyrus fornicatus; H, gyrus hippocampi; h, sulcus hippocampi; U, uncinate gyrus; cm, calloso-marginal fissure; F1, median aspect of first frontal convolution; c, terminal portion of sulcus centralis (fissure of Rolando); A, ascending frontal; B, ascending parietal convolution; P1' præcuneus; Oz, cuneus; po, parieto-occipital fissure; o, sulcus occipitalis transversus; oc, calcarine fissure; oc', superior; oc", inferior ramus of the same; D, gyrus descendens; T4, gyrus occipito-temporalis lateralis (lobulus fusiformis); T5, gyrus occipito-temporalis medialis (lobulus lingualis) (Ecker).

The following is a brief summary of the appearances presented by the several layers.

(1). A number of horizontal transverse and oblique nerve-fibres.

(2). A very pale layer containing very few nerve-cells and fibres.

(3). A layer containing many nerve-cells, both oval and angular.

(4). A pale thicker layer consisting of large pyramidal cells with their bases downwards and their apices towards the free surface, interspersed with radiating bundles of nerve-fibres.

(5). A narrower stratum with many irregular corpuscles, like those in the cerebellum.

(6). A broader layer with many irregular and fusiform cells.

Some of the above are shown in the accompanying drawing; especially the oval, and the large pyramidal cells and the small corpuscles.

Fig. 246.*

The white matter of the brain, as of the spinal cord, consists of bundles of medullated, and, in the neighbourhood of the grey matter, of non-medullated nerve-fibres, which are held together by delicate connective tissue. The size of the fibres of the brain is usually less than that of the fibres of the spinal cord; the average diameter of the former being about $\frac{1}{10,000}$ of an inch

Chemical Composition of Grey and White Matter.

The chemistry of nerves and nerve-cells has been chiefly studied in the brain and spinal cord. Nerve-matter contains several albuminous bodies (cerebrin, lecithin, and some others), also fatty matter, which can be extracted by ether (including cholesterin), and various salts, especially phosphates of Potassium and Magnesium, which exist in larger quantity than those of Sodium and Calcium. Yolk of egg resembles cerebral substance very closely in its chemical composition; milk and muscle also come very near it.

* Fig. 246. Section of cerebrum; *p m*, pia mater, sending down *c*, capillaries, into the grey matter; *n c*, nerve-cells, strongly nucleated, lodged in clear spaces in the neuroglia; *p c*, pyramidal cells highly characteristic of the cerebrum; they receive two processes at their inferior angles, and give off one process upwards towards the free surface (Schofield).

An important point to be noted in the composition of nerve-matter, is the proportion of water it contains, which to some extent is an index of its activity. White matter contains about 70 per cent., while grey matter contains as much as 86 per cent., *i.e.*, a considerably larger proportion than the blood. Moreover, brain-substance in children is considerably more watery than in adults. Brain-matter has also a great power of taking up water, and can even double its bulk by imbibition.

Functions of the Cerebrum.

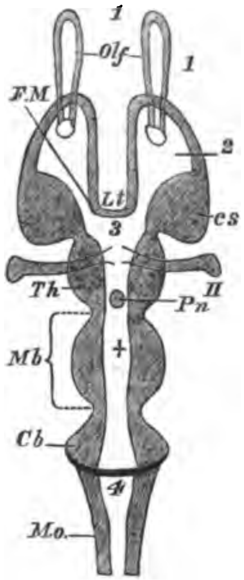
(1). The Cerebral hemispheres are the organs by which are perceived those clear and more impressive sensations which can be retained, and regarding which we can judge. (2). The Cerebrum is the organ of the will, in so far at least as each act of the will requires a deliberate, however quick determination. (3). It is the means of retaining impressions of sensible things, and reproducing them in subjective sensations and ideas. (4). It is the medium of all the higher emotions and feelings, and of the faculties of judgment, understanding, memory, reflection, induction, imagination, and the like.

Evidence regarding the physiology of the cerebral hemispheres has been obtained, as in the case of other parts of the nervous system, from the study of Comparative Anatomy, from Pathology, and from Experiments on the lower animals.

The chief evidences regarding the functions of the Cerebral hemispheres derived from these various sources, are briefly these:—1. Any severe injury of them, such as a general concussion, or sudden pressure by apoplexy, may instantly deprive a man of all power of manifesting externally any mental faculty. 2. In the same general proportion as the higher mental faculties are developed in the vertebrate animals, and in man at different ages and in different individuals, the more is the size of the cerebral hemispheres developed in comparison with the rest of the cerebro-spinal system. 3. No other part of the nervous system bears a corresponding proportion to the development of the mental faculties. 4. Congenital and other morbid defects of the cerebral hemisphere are, in general, accompanied by corresponding deficiency in the range or power of the intellectual faculties and the higher instincts. 5. Removal of the cerebral hemispheres in one of the lower animals produces effects corres-

ponding with what might be anticipated from the foregoing facts. The animal, although retaining sensation, and the power of performing even complicated reflex acts, remains in a state of stupor, and performs no voluntary movement of any kind. (See below.)

Fig. 247.*



The great relative and absolute size of the cerebral hemispheres in the adult man, mask to a great extent the real arrangement of the several parts of the brain, which is illustrated in the two accompanying diagrams.

From these it is apparent that the parts of the brain are disposed in a linear series, as follows (from before backwards): olfactory lobes, cerebral hemispheres, optic thalami, and third ventricle, corpora quadrigemina, or optic lobes, cerebellum, medulla oblongata.

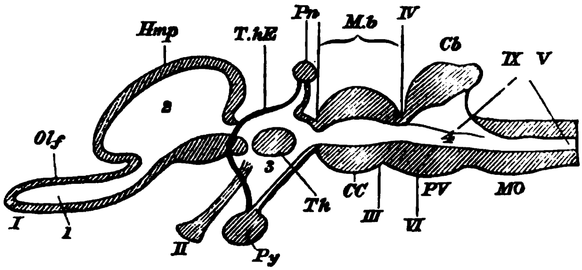
This linear arrangement of parts actually occurs in the human fœtus (see Chapter on Development), and it is permanent in some of the lower Vertebrata, *e.g.*, Fishes, in which the cerebral hemispheres are represented by a pair of ganglia intervening between the olfactory and the optic lobes, and considerably smaller than the latter. In Amphibia the cerebral lobes are further developed, and are larger than any of the other ganglia.

In Reptiles and Birds the cerebral ganglia attain a still further development, and in Mammalia the cerebral hemispheres exceed in weight all the rest of the brain. As we ascend the scale, the relative size of the cerebrum increases, till in the higher apes and man the hemispheres, which commenced as two little lateral buds from the anterior cerebral vesicle, have grown upwards and backwards, completely covering in and hiding from view all the rest of the brain. At the same time the smooth surface of the brain, in many lower Mammalia, such as the rabbit, is replaced by the labyrinth of convolutions of the human brain.

* Fig. 247. Diagrammatic horizontal section of a Vertebrate brain. *The figures serve both for this and the next diagram. Mb*, mid brain: what lies in front of this is the fore-, and what lies behind, the hind-brain; *Lt*, lamina terminalis; *Olf*, olfactory lobes; *Hmp*, hemispheres; *Th.E*, thalamencephalon; *Pn*, pineal gland; *Py*, pituitary body; *FM*, foramen of Munro; *cs*, corpus striatum; *Th*, optic thalamus; *CC*, crura cerebri: the mass lying above the canal represents the corpora quadrigemina; *Cb*, cerebellum; *I—IX.*, the nine pairs of cranial nerves; 1, olfactory ventricle; 2, lateral ventricle; 3, third ventricle; 4, fourth ventricle; +, iter a tertio ad quartum ventriculum, (Huxley).

The brain of an adult man weighs from 48 to 50 oz.—or about 3 lbs. It exceeds in absolute weight that of all the lower animals except the elephant and whale. Its weight, *relatively to that of the body*, is only exceeded by that of a few small birds and some of the smaller monkeys. In the adult man it ranges from $\frac{1}{35}$—$\frac{1}{50}$ of the body-weight.

Fig. 248.*



Age.—In a new-born child the brain (weighing 10—14 oz.) is $\frac{1}{10}$ of the body weight. At the age of 7 years the weight of the brain already averages 40 oz., and about 14 years the brain not unfrequently reaches the weight of 48 oz.

Beyond the age of 40 years the weight slowly but steadily declines at the rate of about 1 oz. in 10 years.

Sex.—The average weight of the female brain is less than the male ; and this difference persists from birth throughout life. In the adult it amounts to about 5 oz. Thus the average weight of an adult woman's brain is about 44 oz.

Intelligence.—The brain of Cuvier weighed 64 oz., that of Dr. Abercrombie 63 oz., that of Goodsir 57½, that of Sir J. Simpson 54 oz.

The brains of idiots are generally much below the average, some weighing less than 16 oz. Still the facts at present collected do not warrant more than a very general statement, to which there are numerous exceptions, that the brain weight corresponds to some extent with the degree of intelligence. There can be little doubt that the *complexity* and *depth* of the convolutions, which indicate the area of the grey matter of the cortex, correspond with the degree of intelligence (R. Wagner).

The *spinal cord* of man weighs from 1—1½ oz.; its weight relatively to the brain is about 1:36. As we descend the scale, this ratio constantly increases till in the mouse it is 1:4. In cold-blooded animals the relation is reversed, the spinal cord is the heavier and the more important organ. In the newt, 2:1 ; and in the lamprey, 75:1.

Distinctive Characters of the Human Brain.

The following characters distinguish the brain of man and apes from those of all other animals.

* Fig. 248. Longitudinal and vertical diagrammatic section of a *Vertebrate brain.* Letters as before. Lamina terminalis is represented by the strong black line joining *Pn* and *Py* (Huxley).

(*a*). The rudimentary condition of the olfactory lobes.
(*b*). A perfectly defined fissure of Sylvius.
(*c*). A posterior lobe completely covering the cerebellum.
(*d*). The presence of posterior cornua in the lateral ventricles (Gratiolet).

The most distinctive points in the human brain, as contrasted with that of apes, are:

(1). The much greater size and weight of the whole brain. The brain of a full-grown gorilla weighs only about 15 oz., which is less than ⅓ the weight of the human adult male brain, and barely exceeds that of the human infant at birth.

(2). The much greater complexity of the convolutions, especially the existence in the human brain of tertiary convolutions in the sides of the fissures.

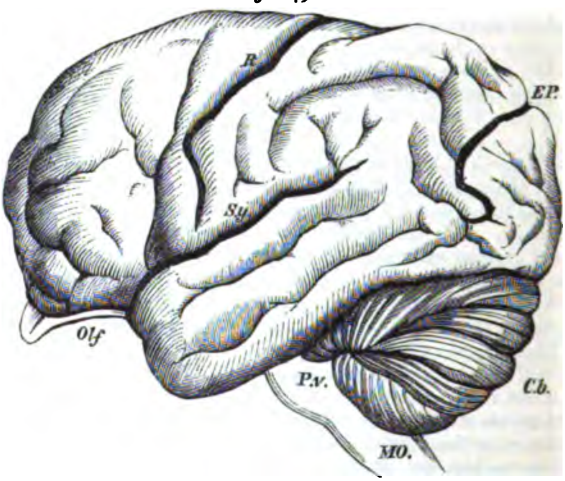
(3). The greater relative size and complexity, and the blunted quadrangular contour of the frontal lobes in man, which are relatively both broader, longer, and higher, than in apes.

In apes the frontal lobes project keel-like (rostrum) between the olfactory bulbs.

(4). The much greater prominence of the temporo-sphenoidal lobe in apes.

(5). The fissure of Sylvius is nearly horizontal in man, while in apes it slants considerably upwards.

Fig. 249.*



* Fig. 249. Brain of the Orang, ⅔ natural size, showing the arrangement of the convolutions. *Sy*, fissure of Sylvius; *R*, fissure of rolando; *E P*, external perpendicular fissure; *Olf*, olfactory lobe; *Cb*, cerebellum; *P V*, pons Varolii; *M O*, medulla oblongata. As contrasted with the human brain, the frontal lobe is short and small relatively, the fissure of Sylvius is oblique, the temporo-sphenoidal lobe very prominent, and the external perpendicular fissure very well marked (Gratiolet).

(6). The distinctness of the external perpendicular fissure, which in apes is a well-defined almost vertical "slash," while in man it is almost obscured by the annectent gyri (Rolleston).

Most of the above points are shown in the accompanying figure of the brain of the Orang.

Effects of the Removal of the Cerebrum.

The removal of the cerebrum in the lower animals appears to reduce them to the condition of a mechanism without spontaneity. A pigeon from which the cerebrum has been removed will remain motionless and apparently unconscious unless disturbed. When disturbed in any way it soon recovers its former position; when thrown into the air it flies.

In the case of the frog, when the cerebral lobes have been removed, the animal appears similarly deprived of all power of spontaneous movement. But it sits up in a natural attitude, breathing quietly; when pricked it jumps away; when thrown into the water it swims; when placed upon the palm of the hand it remains motionless, although, if the hand be gradually tilted over till the frog is on the point of losing his balance, he will crawl up till he regains his equilibrium, and comes to be perched quite on the edge of the hand. This condition contrasts with that resulting from the removal of the entire brain, leaving only the spinal cord; in this case only the simpler reflex actions can take place. The frog does not breathe, he lies flat on the table instead of sitting up; when thrown into a vessel of water he sinks to the bottom; when his legs are pinched he kicks out, but does not leap away.

Respecting the mode in which the brain discharges its functions, there is no evidence whatever. But it appears that, for all but its highest intellectual acts, one of the cerebral hemispheres is sufficient. For numerous cases are recorded in which no mental defect was observed, although one cerebral hemisphere was so disorganised or atrophied that it could not be supposed capable of discharging its functions. The remaining hemisphere was, in these cases, adequate to the functions generally discharged by both; but the mind does not seem in any of these cases to

have been tested in very high intellectual exercises; so that it is not certain that one hemisphere will suffice for these. In general, the mind combines, as one sensation, the impressions which it derives from one object through both hemispheres, and the ideas to which the two such impressions give rise are single.

In relation to common sensation and the effort of the will, the impressions to and from the hemispheres of the brain are carried across the middle line; so that in destruction or compression of either hemisphere, whatever effects are produced in loss of sensation or voluntary motion, are observed on the side of the body opposite to that on which the brain is injured.

In speaking of the cerebral hemispheres as the so-called organs of the mind, they have been regarded as if they were single organs, of which all parts are equally appropriate for the exercise of each of the mental faculties. But it is possible that each faculty has a special portion of the brain appropriated to it as its proper organ. For this theory the principal evidences are as follow:—1. That it is in accordance with the physiology of the other compound organs or systems in the body, in which each part has its special function; as, for example, of the digestive system, in which the stomach, liver, and other organs perform each their separate share in the general process of the digestion of the food. 2. That in different individuals the several mental functions are manifested in very different degrees. Even in early childhood, before education can be imagined to have exercised any influence on the mind, children exhibit various dispositions—each presents some predominant propensity, or evinces a singular aptness in some study or pursuit; and it is a matter of daily observation that every one has his peculiar talent or propensity. But it is difficult to imagine how this could be the case, if the manifestation of each faculty depended on the whole of the brain: different conditions of the whole mass might affect the mind generally, depressing or exalting all its functions in an equal degree, but could not permit one faculty to be strongly and another weakly manifested. 3. The plurality of organs in the brain is supported by the phenomena of some forms of mental derangement. It is not usual for all the mental faculties

in an insane person to be equally disordered; it often happens that the strength of some is increased, while that of others is diminished; and in many cases one function only of the brain is deranged, while all the rest are performed in a natural manner. 4. The same opinion is supported by the fact that the several mental faculties are developed to their greatest strength at different periods of life, some being exercised with great energy in childhood, others only in adult age; and that, as their energy decreases in old age, there is not a gradual and equal diminution of power in all of them at once, but, on the contrary, a diminution in one or more, while others retain their full strength, or even increase in power. 5. The plurality of cerebral organs appears to be indicated by the phenomena of dreams, in which only a part of the mental faculties are at rest or asleep, while the others are awake, and, it is presumed, are exercised through the medium of the parts of the brain appropriated to them.

Unconscious Cerebration.—In connection with the above, some remarkable phenomena should be mentioned which have been described as depending on an *unconscious* action of the brain.

It must be within the experience of every one to have tried to recollect some particular name or occurrence: and after trying in vain for some time the attempt is given up and quite forgotten amid other occupations, when suddenly, hours or even a day or two afterwards, the desired name or occurrence unexpectedly flashes across the mind. Such occurrences are supposed by many to be due to the requisite cerebral processes going on unconsciously, and, when the result is reached, to our all at once becoming conscious of it.

That such *unconscious cerebration* may sometimes occur, is likely enough; and it is paralleled by the unconscious walking of a somnambulist. But many cases of so-called unconscious cerebration are better explained by the supposition that some missing link in the chain of reasoning cannot at the moment be found; but is afterwards, by some chance combination of events, suggested, and thus the mental process is at once, with the memory of what has gone before, completed.

Again, in the vain endeavour to solve a difficult or it may be an easy problem, the reasoner is frequently in the condition of a man whose wearied muscles could never, before they have rested, overcome some obstacle. In both cases,—of brain and muscle, after renewal of their textures by rest, the task is performed so rapidly as to seem instantaneous.

From the apparently greater frequency of interference with the faculty of speech in disease of the *left* than of the *right* half of the cerebrum, it has been thought that the nerve-centre for

language, including in this term all articulate expression of ideas, is situate in the *left* cerebral hemisphere. A large number of cases are on record in which *aphasia*, or the loss of power of expressing ideas in words, has been associated with disease of the posterior part of the lower or third frontal convolution on the left side (Hughlings Jackson, Broca). This condition is usually associated with paralysis of the right side (right hemiplegia). The only conclusion, however, which can be drawn from this, is, that the integrity of this particular convolution is essential to the faculty of speech; we cannot conclude that it is necessarily the *centre* for language. It may be only one link in the complete chain of nervous connections necessary for the translation of an idea into articulate expression.

It seems highly probable that the corresponding right convolution can take on the same functions as the left; and it is in this way that we can explain those cases in which recovery of speech takes place, though the *left* frontal convolution still remains diseased.

Nothing is known of the function of the pineal and pituitary glands. They have been, indeed, supposed by some to be rather ductless glands than nervous organs (p. 422).

For many years the only attempt to localize different functions in definite regions of the brain, was that of Gall and Spurzheim; but their phrenological system is destitute of any scientific basis, either of experiment, pathological observation, or comparative anatomy. Quite recently, however, attempts have been made to localize cerebral functions by means of experiments on the lower animals.

It had long been well-known that the cerebral hemispheres could not be excited by mechanical, chemical, or thermic stimuli, but Fritsch and Hitzig were the first to show that they are amenable to electric irritation. They employed a weak constant current in their experiments, applying a pair of fine electrodes not more than $\frac{1}{12}$ in. apart to different parts of the cerebral cortex. The results thus obtained have been confirmed and extended by Dr. Ferrier.

The following are the fundamental phenomena observed in all these cases:

(1). Excitation of the same spot is always followed by the same movement in the same animal. (2). The area of excitability for any given movement is extremely small, and admits of very accurate definition. (3). In different animals excitations of anatomically corresponding spots produce similar or corresponding results (Burdon-Sanderson).

The various definite movements resulting from the electric stimulation of

circumscribed areas of the cerebral cortex, are enumerated in the description of the accompanying figures of the dog and monkey's brain.

In the case of the dog, the results obtained are summed up as follows, by Hitzig.

(*a*). One portion (anterior) of the convexity of the cerebrum is motor; another portion (posterior) is non-motor. (*b*). Electric stimulation of the motor portion produces co-ordinated muscular contraction on the opposite side of the body. (*c*). With very weak currents, the contractions produced are distinctly limited to particular groups of muscles; with stronger currents the stimulus is communicated to other muscles of the same or neighbouring parts. (*d*). The portions of the brain intervening between these motor centres are inexcitable by similar means.

Fig. 250.*

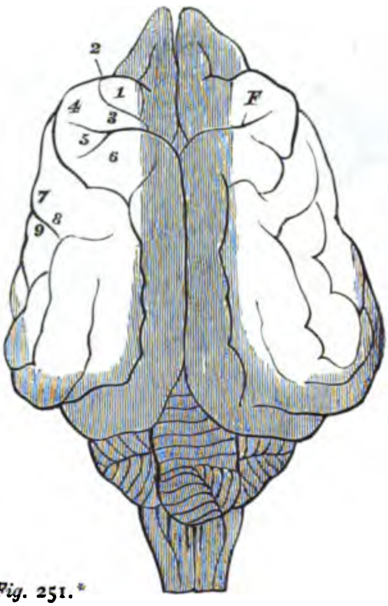
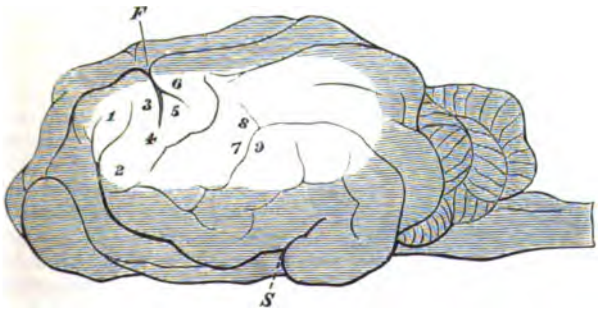


Fig. 251.*



* Figs. 250 and 251. Brain of dog, viewed from above and in profile. *F*, frontal fissure, sometimes termed crucial sulcus, corresponding to the fissure of Rolando in man; *S*, fissure of Sylvius, around which the four longitudinal convolutions are concentrically arranged; 1, flexion of head on the neck, in the median line; 2, flexion of head on the neck, with rotation towards the side of the stimulus; 3, 4, flexion and extension of anterior limb; 5, 6, flexion and extension of posterior limb; 7, 8, 9, contraction of orbicularis oculi, and the facial muscles in general. The unshaded part is that exposed by opening the skull (Dalton).

With regard to the facts above mentioned, all experimenters are agreed, but there is still considerable diversity of opinion as to their explanation.

Fig. 252.*

It is evident that the spots marked out on the cortex are not strictly speaking motor *centres*, for they can be removed entirely without destroying the power of voluntary motion.

Dr. Burdon-Sanderson has shown that electric stimulation of different points in a horizontal section, through the deeper parts of the hemispheres, produces the same effects as stimulation of the so-called "centres" in the grey matter overlying them: while the same results follow electric stimulation of different points of the corpus striatum.

Fig. 253.*

In applying the facts ascertained by these experiments to elucidate the physiology of the human brain, we must remember that the method of electric stimu-

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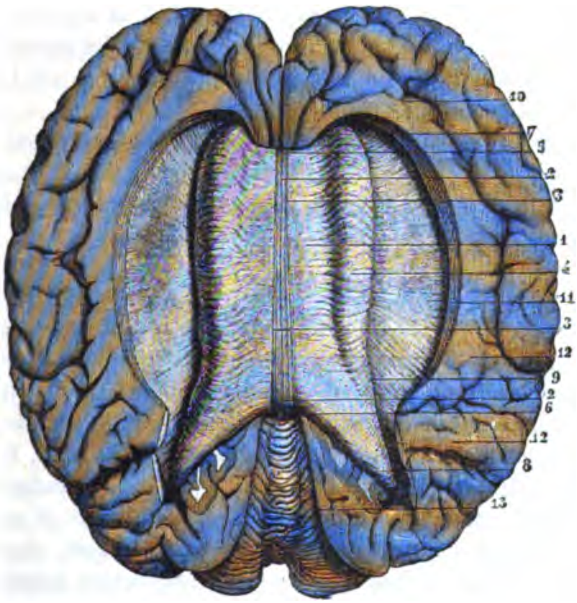
* Figs. 252 and 253. Diagrams of monkey's brain to show the effects of electric stimulation of certain spots. 1, movement of hind foot; 2, chiefly adduction of foot; 3, movements of hind foot and tail; 4, of latissimus dorsi; 5, extension forward of arm; *a, b, c, d*, movements of hand and wrist; 6, supination and flexion of forearm; 7, elevation of upper lip; 8, conjoint action of elevation of upper lip and depression of lower; 9, opening of mouth and protrusion of tongue; 10, retraction of tongue; 11, action of platysma; 12, elevation of eyebrows and eyelids, dilatation of pupils, and turning head to opposite side; 13, eyes directed to opposite side and upwards, with usually contraction of the pupils; 13′, similar action, but eyes usually directed downwards; 14, retraction of opposite ear, head turns to the opposite side, the eyes widely opened and pupils dilated; 15, stimulation of this region, which corresponds to the tip of the uncinate convolution, causes torsion of the lip and nostril of the same side (Ferrier).

lation is an artificial one, differing widely from the ordinary stimuli to which the brain is subject during life.

Of the physiology of the other parts of the brain, little or nothing can be said.

Fig. 254.*



Of the offices of the *corpus callosum*, or great transverse and oblique commissure of the brain, nothing positive is known.

* Fig. 254. View of the corpus callosum from above. ½.—The upper surface of the corpus callosum has been fully exposed by separating the cerebral hemispheres and throwing them to the side; the gyrus fornicatus has been detached, and the transverse fibres of the corpus callosum traced for some distance into the cerebral medullary substance. 1, the upper surface of the corpus callosum; 2, median furrow or raphe; 3, longitudinal striæ bounding the furrow; 4, swelling formed by the transverse bands as they pass into the cerebrum; 5, anterior extremity or knee of the corpus callosum; 6, posterior extremity; 7, anterior, and 8, posterior part of the mass of fibres proceeding from the corpus callosum; 9, margin of the swelling; 10, anterior part of the convolution of the corpus callosum; 11, hem or band of union of this convolution; 12, internal convolutions of the parietal lobe; 13, upper surface of the cerebellum (Sappey after Foville).

But instances in which it was absent, or very deficient, either without any evident mental defect, or with only such as might be ascribed to coincident affections of other parts, make it probable that the office which is commonly assigned to it, of enabling the two sides of the brain to act in concord, is exercised only in the highest acts of which the mind is capable. And this view is confirmed by the very late period of its development, and by its very rudimentary condition (Flower) in all but the placental Mammalia.*

To the fornix and other commissures no special function can be assigned; but it is a reasonable hypothesis that they connect the action of the parts between which they are severally placed.

Sleep.

All parts of the body which are the seat of active change require periods of rest. The alternation of work and rest is a necessary condition of their maintenance and of the healthy performance of their functions. These alternating periods, however, differ much in duration in different cases; but, for any individual instance, they preserve a general and rather close uniformity. Thus, as before mentioned, the periods of rest and work, in the case of the heart, occupy, each of them, about half a second; in the case of the ordinary respiratory muscles the periods are about four or five times as long. In many cases, again (as of the voluntary muscles during violent exercise) while the periods during active exertion alternate very frequently, yet the expenditure goes far ahead of the repair, and, to compensate for this, an after repose of some hours becomes necessary; the rhythm being less perfect as to *time*, than in the case of the muscles concerned in circulation and respiration.

Obviously, it would be impossible that, in the case of the Brain, there should be short periods of activity and repose, or in other words, of consciousness and unconsciousness. The

* See cases of congenital deficiency of the corpus callosum, by Sir J. Paget and Mr. Henry in the twenty-ninth and thirty-first volumes of the Medico-Chirurgical Transactions.

repose must occur at long intervals; and it must therefore be proportionately long. Hence the necessity for that condition which we call *Sleep;* a condition which seeming at first sight exceptional, is only an unusually perfect example of what occurs, at varying intervals, in every actively working portion of our bodies.

A temporary abrogation of the functions of the cerebrum imitating sleep, may occur, in the case of injury or disease, as the consequence of two apparently widely different conditions. Insensibility is equally produced by a *deficient* (see Syncope, p. 188), and an *excessive* quantity of blood within the cranium, (coma); but it was once supposed that the latter offered the truest analogy to the normal condition of the brain in sleep, and in the absence of any proof of the contrary, the brain was said to be during sleep, *congested.* Direct experimental enquiry has led, however, to the opposite conclusion.

By exposing, at a circumscribed spot, the surface of the brain of living animals, and protecting the exposed part by a watch-glass, Mr. Durham was able to prove that the brain becomes visibly paler (anæmic) during sleep; and the anæmia of the optic disc during sleep, observed by Dr. Hughlings Jackson, may be taken as a strong confirmation, by analogy, of the same fact.

A very little consideration will show that these experimental results correspond exactly with what might have been foretold from the analogy of other physiological conditions. Blood is supplied to the brain for two partly distinct purposes. (1.) It is supplied for mere nutrition's sake. (2.) It is necessary for bringing supplies of potential or active energy, (*i.e.*, either *combustible matter* or *heat*) which may be transformed by the cerebral corpuscles into the various manifestations of nerve-force. During sleep, blood is requisite for only the first of these purposes; and its supply in greater quantity would be not only useless, but, by supplying an excitement to work, when rest is needed, would be positively harmful. In this respect the varying circulation of blood in the brain exactly resembles that which occurs in all other energy transforming parts of the body; *e. g. glands* or *muscles.*

What we term *sleep* occurs often in very different degrees in different parts of the nervous system; and in some parts the expression cannot be used in the ordinary sense.

The medulla oblongata, it has been said, "never sleeps." But this is only "true in a false sense." The same thing might be said of the heart (p. 166) or other parts which have short rhythmic periods of repose; and even thus the remark applies only to the nerve-centres engaged in circulation and respiration.

The phenomena of *dreams* and *somnambulism* are examples of differing degrees of sleep in different parts of the cerebro-spinal nervous system. In the former case the cerebrum is still partially active; but the mind-products of its action are no longer corrected by the reception, on the part of the sleeping *sensorium* (sensory ganglia, p. 530), of impressions of objects belonging to the outer world; neither can the cerebrum, in this half-awake condition, act on the centres of reflex action of the voluntary muscles, so as to cause the latter to contract—a fact within the painful experience of all who have suffered from nightmare.

In somnambulism the cerebrum is capable of exciting that train of reflex nervous action which is necessary for progression, while the nerve-centre of *muscular sense* (in the cerebellum ?) is, presumably, fully awake; but the *sensorium* is still asleep, and impressions made on it are not sufficiently *felt* to rouse the cerebrum to a comparison of the difference between mere ideas or memories and sensations derived from external objects.

PHYSIOLOGY OF THE CRANIAL NERVES.

The *cranial* nerves are commonly enumerated as nine pairs; but the number is in reality twelve, the seventh nerve consisting, as it does, of two nerves, and the eighth of three. All arise (superficial origin) from the base of the encephalon, in a double series which extends from the under surface of the anterior cerebral lobes to the lower end of the medulla oblongata. Traced into the substance of the brain and medulla, the roots of the nerves are found connected with various masses of grey matter, which are all connected one with another, and with the cerebral hemispheres.

The roots of the olfactory *tracts* are connected deeply with the cortex of the anterior cerebral hemisphere, and probably with the corpora striata also. The optic nerves can be traced into the optic thalami, corpora quadrigemina, and corpora geniculata. The third and fourth nerves arise from grey matter beneath the corpora quadrigemina; and the roots of origin of the remainder of the cranial nerves can be traced to grey matter in the medulla oblongata beneath the floor of the fourth ventricle, and in the more central part of the medulla, around its central canal, as low down as the decussation of the pyramids.

According to their several functions, the cranial nerves may be thus arranged :—

Nerves of special sense .	Olfactory, optic, auditory, part of the glosso-pharyngeal, and of the lingual branch of the fifth.
„ of common sensation	The greater portion of the fifth.
„ of motion	Third, fourth, lesser division of the fifth, sixth, facial, and hypoglossal.
Mixed nerves	Glossopharyngeal, pneumogastric, and spinal accessory.

The physiology of the several nerves of the special senses will be considered with the organs of those senses.

Third Nerve.—The third nerve, or *motor oculi*, supplies the levator palpebræ superioris muscle, and, of the muscles of the eye-ball, all but the superior oblique or trochlearis, to which the fourth nerve is appropriated, and the rectus externus which receives the sixth nerve. Through the medium of the ophthalmic or lenticular ganglion, of which it forms what is called the short root, it also supplies motor filaments to the iris and ciliary muscle.

When the third nerve is irritated within the skull, all those muscles to which it is distributed are convulsed. When it is paralyzed or divided, the following effects ensue : (1), the upper eyelid can be no longer raised by the levator palpebræ, but droops (ptosis) and remains gently closed over the eye. under the unbalanced influence of the orbicularis palpebrarum, which is supplied by the facial nerve : (2), the eye is turned outwards (external strabismus) by the unbalanced action of the rectus externus, to which the sixth nerve is appropriated : and hence, from the irregularity of the axes of the eyes, double-sight is often experienced when a single object is within view of both the eyes : (3), the eye cannot be moved either upwards, downwards, or inwards: (4), the pupil becomes dilated (mydriasis), and insensible to light : (5), the eye cannot "accommodate" itself for vision at short distances.

The relation of the third nerve to the iris is of peculiar interest. In ordinary circumstances the contraction of the iris is a reflex action, which may be explained as produced by the stimulus of light on the retina being conveyed by the optic nerve to the brain (probably to the corpora quadrigemina), and thence reflected through the third nerve to the iris. Hence the iris ceases to act when either the optic or the third nerve is divided or destroyed, or when the corpora quadrigemina are destroyed or much compressed. But when the optic nerve is divided, the contraction of the iris may be excited by irritating that portion of the nerve which is connected with the brain; and when the third nerve is divided, the irritation of its distal portion will still excite contraction of the iris.

The contraction of the iris thus shows all the characters of a reflex act, and in ordinary cases requires the concurrent action of the optic nerve, corpora quadrigemina, and third nerve; and, probably also, considering the peculiarities of its perfect mode of action, the ophthalmic ganglion. But, besides, both irides will contract their pupils under the reflected stimulus of light falling only on one retina or under irritation of one optic nerve. Thus, in amaurosis of one eye, its pupil may contract when the other eye is exposed to a stronger light: and generally the contraction of each of the pupils appears to be in direct proportion to the total quantity of light which stimulates either one or both retinæ, according as one or both eyes are open.

The iris acts also in association with certain other muscles supplied by the third nerve: thus, when the eye is directed inwards, or upwards and inwards, by the action of the third nerve distributed in the rectus internus and rectus superior, the iris contracts, as if under direct voluntary influence. The will cannot, however, act on the iris alone through the third nerve; but this aptness to contract in association with the other muscles supplied by the third, may be sufficient to make it act even in total blindness and insensibility of the retina, whenever these muscles are contracted. The contraction of the pupils, when the eyes are moved inwards, as in looking at a near object, has probably the purpose of excluding those outermost rays of light which would be too far divergent to be refracted to a clear image on the retina; and the dilatation in looking straight forwards, as in looking at a distant object, permits the admission of the largest number of rays, of which none are too divergent to be so refracted.

Fourth Nerve.—The fourth nerve, or *Nervus trochlearis* or *patheticus*, is exclusively motor, and supplies only the trochlearis or obliquus superior muscle of the eyeball.

Physiology of the Fifth or Trigeminal Nerve.

Fifth or Trigeminal nerve.—The fifth or trigeminal nerve resembles, as already stated, the spinal nerves, in that its branches are derived through two roots; namely, the larger or *sensory*, in connection with which is the Gasserian ganglion, and the smaller or *motor* root which has no ganglion, and which

passes under the ganglion of the sensory root to join the third branch or division which issues from it. The first and second divisions of the nerve, which arise wholly from the larger root, are purely sensory. The third division being joined, as before said, by the motor root of the nerve, is of course both motor and sensory.

Fig. 255.*

* Fig. 255. General plan of the branches of the fifth pair (after a sketch by Sir Charles Bell). ½.—1, lesser root of the fifth pair; 2, greater root passing forwards into the Gasserian ganglion; 3, placed on the bone above the ophthalmic nerve, which is seen dividing into the supraorbital, lachrymal, and nasal branches, the latter connected with the ophthalmic ganglion; 4, placed on the bone close to the foramen rotundum, marks the superior maxillary division, which is connected below with the spheno-palatine ganglion, and passes forwards to the infraorbital foramen; 5, placed on the bone over the foramen ovale, marks the inferior maxillary nerve, giving off the anterior auricular and muscular branches, and continued by the inferior dental to the lower jaw, and by the gustatory to the tongue; *a*, the submaxillary gland, the submaxillary ganglion placed above it in connection with the gustatory nerve; 6, the chorda tympani; 7, the facial nerve issuing from the stylo-mastoid foramen.

Through the branches of the greater or ganglionic portion of the fifth nerve, all the anterior and antero-lateral parts of the face and head, with the exception of the skin of the parotid region (which derives branches from the cervical spinal nerves), acquire common sensibility; and among these parts may be included the organs of special sense, from which common sensations are conveyed through the fifth nerve, and their special sensations through their several nerves of special sense. The muscles, also, of the face and lower jaw acquire muscular sensibility through the filaments of the ganglionic portion of the fifth nerve distributed to them with their proper motor nerves.

Through branches of the lesser or non-ganglionic portion of the fifth, the muscles of mastication, namely, the temporal, masseter, two pterygoid, anterior part of the digastric, and mylo-hyoid, derive their motor nerves. Filaments are also supplied to the tensor tympani and tensor palati.

The motor function of these branches is proved by the violent contraction of all the muscles of mastication in experimental irritation of the third or inferior maxillary division of the nerve; by paralysis of the same muscles, when it is divided or disorganised, or from any reason deprived of power; and by the retention of the power of these muscles, when all those supplied by the facial nerve lose their power through paralysis of that nerve. The last instance proves best, that though the buccinator muscle gives passage to, and receives some filaments from, a buccal branch of the inferior division of the fifth nerve, yet it derives its motor power from the facial, for it is paralyzed together with the other muscles that are supplied by the facial, but retains its power when the other muscles of mastication are paralyzed. Whether, however, the branch of the fifth nerve which is supplied to the buccinator muscle is entirely sensory, or in part motor also, must remain for the present doubtful. From the fact that this muscle, besides its other functions, acts in concert or harmony with the muscles of mastication, in keeping the food between the teeth, it might be supposed from analogy, that it would have a motor branch from the same nerve that supplies them. There can be no doubt, however, that the so-called buccal branch of the fifth is, in the main, sensitive; although it is not quite certain that it does not give a few motor filaments to the buccinator muscle.

(1). The sensory function of the branches of the greater division of the fifth nerve is proved by all the usual evidences, such as their distribution in parts that are sensitive and not capable of muscular contraction, the exceeding sensibility of some of these parts, their loss of sensation when the nerve is paralyzed or

divided, the pain without convulsions produced by morbid or experimental irritation of the trunk or branches of the nerve, and the analogy of this portion of the fifth to the posterior root of the spinal nerve.

But although formed of sensory filaments exclusively, the branches of the greater or ganglionic portion of the fifth nerve exercise: (2), a manifold influence on the movements of the muscles of the head and face, and other parts in which they are distributed. They do so, in the first place (*a*), by providing the muscles themselves with that sensibility without which the mind, being unconscious of their position and state, cannot voluntarily exercise them. It is, probably, for conferring this sensibility on the muscles, that the branches of the fifth nerve communicate so frequently with those of the facial and hypoglossal, and the nerves of the muscles of the eye; and it is because of the loss of this sensibility that when the fifth nerve is divided, animals are always slow and awkward in the movement of the muscles of the face and head, or hold them still, or guide their movements by the sight of the objects towards which they wish to move.

Again, the fifth nerve has an indirect influence on the muscular movements, by (*b*) conveying sensations of the state and position of the skin and other parts: which the mind perceiving, is enabled to determine appropriate acts. Thus, when the fifth nerve or its infra-orbital branch is divided, the movements of the lips in feeding may cease, or be imperfect.

Sir C. Bell supposed that the motion of the upper lip, in grasping food, depended directly on the infra-orbital nerve; for he found that, after he had divided that nerve on both sides in an ass, it no longer seized the food with its lips, but merely pressed them against the ground, and used the tongue for the prehension of the food. Mr. Mayo corrected this error. He found, indeed, that after the infra-orbital nerve had been divided, the animal did not seize its food with the lip, and could not use it well during mastication, but that it could open the lips. He, therefore, justly attributed the phenomena in Sir C. Bell's experiments to the loss of sensation in the lips; the animal not being able to feel the food, and, therefore, although it had the power to seize it, not knowing how or where to use that power.

The fifth nerve has also (*c*), an intimate connection with muscular movements through the many reflex acts of muscles of

which it is the necessary excitant. Hence, when it is divided and can no longer convey impressions to the nervous centres to be thence reflected, the irritation of the conjunctiva produces no closure of the eye, the mechanical irritation of the nose excites no sneezing.

The fifth nerve, through its ciliary branches and the branch which forms the long root of the ciliary or ophthalmic ganglion, exercises also (*d*), some influence on the movements of the iris.

When the trunk of the ophthalmic portion is divided, the pupil becomes, according to Valentin, contracted in men and rabbits, and dilated in cats and dogs; but in all cases, becomes immovable, even under all the varieties of the stimulus of light. How the fifth nerve thus affects the iris is unexplained; the same effects are produced by destruction of the superior cervical ganglion of the sympathetic, so that, possibly, they are due to the injury of those filaments of the sympathetic which, after joining the trunk of the fifth, at and beyond the Gasserian ganglion, proceed with the branches of its ophthalmic division to the iris; or, as Dr. R. Hall ingeniously suggests, the influence of the fifth nerve on the movements of the iris may be ascribed to the affection of vision in consequence of the disturbed circulation or nutrition in the retina, when the normal influence of the fifth nerve and ciliary ganglion is disturbed. In such disturbance, increased circulation making the retina more irritable might induce extreme contraction of the iris; or, under moderate stimulus of light, producing partial blindness, might induce dilatation: but it does not appear why, if this be the true explanation, the iris should in either case be immovable and unaffected by the various degrees of light.

Furthermore, the morbid effects which division of the fifth nerve produces in the organs of special sense, make it probable that, in the normal state, the fifth nerve exercises (3), some *trophic* influence on all these organs; although, in part, the effect of the section of the nerve is only indirectly destructive by abolishing sensation, and therefore the natural safeguard which leads to the protection of parts from external injury. Thus, after such division, within a period varying from twenty-four hours to a week, the cornea begins to be opaque; then it grows completely white; a low destructive inflammatory process ensues in the conjunctiva, sclerotica, and interior parts of the eye; and within one or a few weeks, the whole eye may be quite disorganised, and the cornea may slough or be penetrated by a large ulcer. The sense of smell (and not merely that of mechanical irritation of the nose), may be at the same time lost, or gravely

impaired; so may the hearing, and commonly, whenever the fifth nerve is paralysed, the tongue loses the sense of taste in its anterior and lateral parts, *i.e.*, in the portion in which the lingual or gustatory branch of the inferior maxillary division of the fifth is distributed.

That complete paralysis of the fifth nerve may be unaccompanied, at least, for a considerable period, by injury to the organs of special sense, with the exception of that portion of the tongue which is supplied by its gustatory branch, is well illustrated by a valuable case recorded by Dr. Althaus.

The loss of the sense of taste is no doubt due (*a*) to the lingual branch of the fifth nerve being a nerve of special sense; partly, also, it is due (*b*), to the fact that this branch supplies, in the anterior and lateral parts of the tongue, a necessary condition for the proper nutrition of that part; while (*c*), it forms also one chief link in the nervous circle for reflex action, in the secretion of saliva (p. 289). But, deferring this question until the glosso-pharyngeal nerve is to be considered, it may be observed that in some brief time after complete paralysis or division of the fifth nerve, the power of all the organs of the special senses may be lost; they may lose not merely their sensibility to common impressions, for which they all depend directly on the fifth nerve, but also their sensibility to their several peculiar impressions for the reception and conduction of which they are purposely constructed and supplied with special nerves besides the fifth. The facts observed in these cases* can, perhaps, be only explained by the influence which the fifth nerve exercises on the nutritive processes in the organs of the special senses. It is not unreasonable to believe, that, in paralysis of the fifth nerve, their tissues may be the seats of such changes as are seen in the laxity, the vascular congestion, œdema, and other affections of the skin of the face and other tegumentary parts which also accompany the paralysis; and that these changes, which may appear unimportant when they affect external parts, are sufficient to destroy that refinement of structure by which the organs of the special senses are adapted to their functions.

* Two of the best cases are published, with analysis of others, by Mr. Dixon, in the *Medico-Chirurgical Transactions*, vol. xxviii.

According to Magendie and Longet, destruction of the eye ensues more quickly after division of the trunk of the fifth beyond the Gasserian ganglion, or after division of the ophthalmic branch, than after division of the roots of the fifth between the brain and the ganglion. Hence it would appear as if the influence on nutrition were conveyed in part through the filaments of the sympathetic, which join the branches of the fifth nerve at and beyond the Gasserian ganglion. That the filaments of the fifth nerve, however, as well as those of the sympathetic, may conduct such influence, appears certain from the cases, including that by Mr. Stanley, in which the source of the paralysis of the fifth nerve was near the brain, or at its very origin, before it receives any communication from the sympathetic nerve.

The existence of ganglia of the sympathetic in connection with all the principal divisions of the fifth nerve where it gives off those branches which supply the organs of special sense—for example, the connection of the ophthalmic ganglion with the ophthalmic nerve at the origin of the ciliary nerves; of the spheno-palatine ganglion with the superior maxillary division, where it gives its branches to the nose and the palate; of the otic ganglion with the inferior maxillary near the giving off of filaments to the internal ear; and of the sub-maxillary ganglion with the lingual branch of the fifth—all these connections suggest that a peculiar and probably conjoint influence of the sympathetic and fifth nerves is exercised in the nutrition of the organs of the special senses; and the results of experiment and disease confirm this by showing that the nutrition of the organs may be impaired in consequence of impairment of the power of either of the nerves.

A possible but doubtful connection between the fifth nerve and the sense of sight, has been thought to be shown in cases in which blows or other injuries implicating the frontal nerve as it passes over the brow, are followed by total blindness in the corresponding eye. In some cases the blindness occurs at once, probably from concussion of the retina; but in others it is very slowly progressive, as if from defective nutrition of the retina, and may be accompanied with inflammatory disorganisation, like that previously referred to (p. 562).* The connection of the fifth nerve with the result must, however, be considered very doubtful.

Sixth Nerve.—The sixth nerve, *Nervus abducens* or *ocularis externus*, is also, like the fourth, exclusively motor, and supplies only the rectus externus muscle.

In several animals it sends filaments to the iris (Radclyffe Hall); and it has probably done so in man, in some instances in which the iris has not been paralysed, while all the other parts supplied by the third nerve were. (Grant.)

* Such a case is recorded by Snabilie in the Nederlandsch *Lancet*, August, 1846.

The rectus externus is convulsed, and the eye is turned outwards, when the sixth nerve is irritated; and the muscle is paralysed when the nerve is divided. In all such cases of paralysis, the eye squints inwards, and cannot be moved outwards.

In its course through the cavernous sinus, the sixth nerve forms larger communications with the sympathetic nerve than any other nerve within the cavity of the skull does. But the import of these communications with the sympathetic, and the subsequent distribution of its filaments after joining the sixth nerve, are quite unknown.

Facial Nerve.—The facial, or *portio dura* of the seventh pair of nerves, is the motor nerve of all the muscles of the face, including the platysma, but not including any of the muscles of mastication already enumerated (p. 560); it supplies, also, the parotid gland, and through the connection of its trunk with the Vidian nerve, by the petrosal nerves, some of the muscles of the soft palate, probably the levator palati and azygos uvulæ; by its tympanic branches it supplies the stapedius and laxator tympani, and, through the otic ganglion, the tensor tympani; through the *chorda tympani* it sends branches to the submaxillary gland and to the lingualis and some other muscular fibres of the tongue; and by branches given off before it comes upon the face, it supplies the muscles of the external ear, the posterior part of the digastricus, and the stylo-hyoideus.

Besides its *motor* influence, the facial is also, by means of the fibres which are supplied to the submaxillary and parotid glands, a so-called *secretory* nerve. For, through the last-named branches, impressions may be conveyed which excite increased secretion of saliva (p. 288).

When the facial nerve is divided, or in any other way paralysed, the loss of power in the muscles which it supplies, while proving the nature and extent of its functions, displays also the necessity of its perfection for the perfect exercise of all the organs of the special senses. Thus, in paralysis of the facial nerve, the orbicularis palpebrarum being powerless, the eye remains open through the unbalanced action of the levator palpebræ; and the conjunctiva, thus continually exposed to the

air and the contact of dust, is liable to repeated inflammation, which may end in thickening and opacity of both its own tissue and that of the cornea. These changes, however, ensue much more slowly than those which follow paralysis of the fifth nerve, and never bear the same destructive character.

The sense of hearing, also, is impaired in many cases of paralysis of the facial nerve; not only in such as are instances of simultaneous disease in the auditory nerves, but in such as may be explained by the loss of power in the muscles of the internal ear. The sense of smell is commonly at the same time impaired through the inability to draw air briskly towards the upper part of the nasal cavities, in which part alone the olfactory nerve is distributed; because, to draw the air perfectly in this direction, the action of the dilators and compressors of the nostrils should be perfect.

Lastly, the sense of taste is impaired, or may be wholly lost, in paralysis of the facial nerve, provided the source of the paralysis be in some part of the nerve between its origin and the giving off of the chorda tympani. This result, which has been observed in many instances of disease of the facial nerve in man, appears explicable by the influence which, through the chorda tympani, it exercises on the movements of the lingualis and the adjacent muscular fibres of the tongue; and on the process of secretion of saliva.

Together with these effects of paralysis of the facial nerve, the muscles of the face being all powerless, the countenance acquires on the paralysed side a characteristic, vacant look, from the absence of all expression: the angle of the mouth is lower, and the paralysed half of the mouth looks longer than that on the other side; the eye has an unmeaning stare. All these peculiarities increase, the longer the paralysis lasts; and their appearance is exaggerated when at any time the muscles of the opposite side of the face are made active in any expression, or in any of their ordinary functions. In an attempt to blow or whistle, one side of the mouth and cheek acts properly, but the other side is motionless, or flaps loosely at the impulse of the expired air; so in trying to suck, one side only of the mouth

acts; in feeding, the lips and cheek are powerless, and food lodges between the cheek and gum.

Glosso-Pharyngeal Nerve.—The glosso-pharyngeal nerves (16, fig. 256), in the enumeration of the cerebral nerves by numbers according to the position in which they leave the cranium, are considered as divisions of the *eighth pair of nerves*, in which term are included with them the pneumogastric and accessory nerves. But the union of the nerves under one term is inconvenient, although in some parts the glosso-pharyngeal and pneumogastric are so combined in their distribution that it is impossible to separate them in either their anatomy or physiology.

The glosso-pharyngeal nerve gives filaments through its tympanic branch (Jacobson's nerve), to the fenestra ovalis, and fenestra rotunda, and the Eustachian tube; also, to the carotid plexus, and, through the petrosal nerve, to the spheno-palatine ganglion. After communicating, either within or without the cranium, with the pneumogastric, and soon after it leaves the cranium, with the sympathetic, digastric branch of the facial, and the accessory nerve, the glosso-pharyngeal nerve parts into the two principal divisions indicated by its name, and supplies the mucous membrane of the posterior and lateral walls of the upper part of the pharynx, the Eustachian tube, the arches of the palate, the tonsils and their mucous membrane, and the tongue as far forwards as the foramen cæcum in the middle line, and to near the tip at the sides and inferior part.

The glosso-pharyngeal nerve contains some motor fibres, together with those of common sensation and the sense of taste.

1. The muscles which receive filaments from the glosso-pharyngeal are the stylo-pharyngei, palato-glossi, and superior constrictor muscles.

Besides being (2) a nerve of common sensation in the parts which it supplies, and a centripetal nerve through which impressions are conveyed to be reflected to the adjacent muscles, the glosso-pharyngeal is also a nerve of special sensation; being the gustatory nerve, or nerve of taste, in all the parts of the tongue and palate to which it is distributed. After many discussions, the question, Which is the nerve of taste?—the

lingual branch of the fifth, or the glosso-pharyngeal?—may be most probably answered by stating that they are both nerves of this special function. For very numerous experiments and cases have shown that when the trunk of the fifth nerve or its lingual branch is paralysed or divided, the sense of taste is completely lost in the superior surface of the anterior and lateral parts of the tongue. The loss is instantaneous after division of the nerve; and, therefore, cannot be ascribed to the defective nutrition of the part, though to this, perhaps, may be ascribed the more complete and general loss of the sense of taste when the whole of the fifth nerve has been paralysed.

But, on the other hand, while the loss of taste in the part of the tongue to which the lingual branch of the fifth nerve is distributed proves that to be a gustatory nerve, the fact that the sense of taste is at the same time retained in the posterior and postero-lateral parts of the tongue, and in the soft palate and its anterior arch, to which (and to some parts of which exclusively) the glosso-pharyngeal is distributed, proves that this also must be a gustatory nerve.

Pneumogastric Nerve.—The *pneumogastric nerve, nervus vagus,* or *par vagum* (1, fig. 256), has, of all the cranial and spinal nerves, the most various distribution, and influences the most various functions, either through its own filaments, or those which, derived from other nerves, are mingled in its branches.

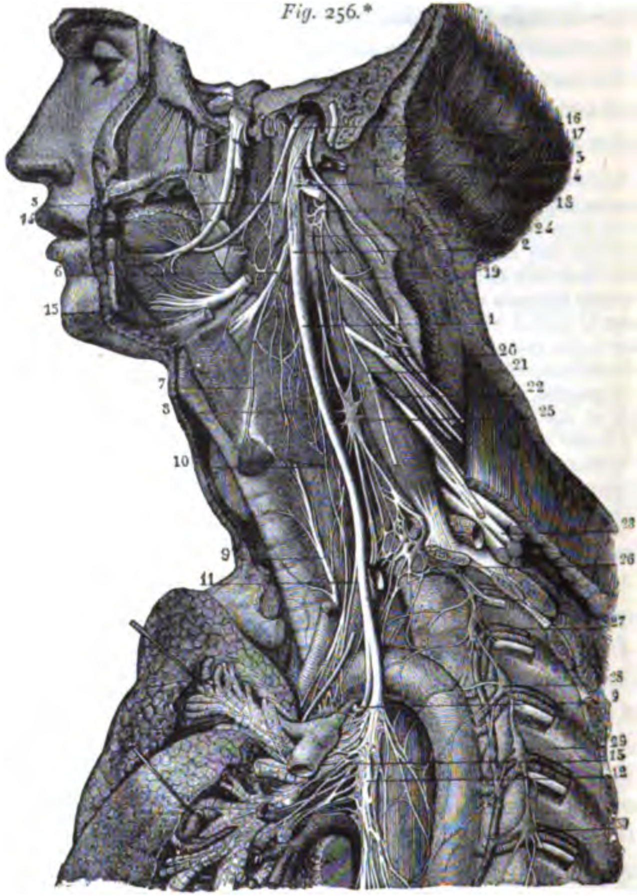
The parts supplied by the branches of the pneumogastric nerve are as follows: by its pharyngeal branches, which enter the pharyngeal plexus, a large portion of the mucous membrane, and, probably, all the muscles of the Pharynx; by the superior laryngeal nerve, the mucous membrane of the under surface of the Epiglottis, the Glottis, and the greater part of the Larynx, and the crico-thyroid muscle; by the inferior laryngeal nerve, the mucous membrane and muscular fibres of the Trachea, the lower part of the pharynx and larynx, and all the muscles of the larynx except the crico-thyroid; by œsophageal branches, the mucous membrane and muscular coats of the Œsophagus. Moreover, the branches of the pneumogastric nerve form a large portion of the supply of nerves to the Heart and the great

Arteries through the cardiac nerves, derived from both the trunk and the recurrent nerve; to the Lungs, through both the anterior and the posterior pulmonary plexuses; and to the Stomach, by its terminal branches passing over the walls of that organ; while branches are also distributed to the Liver and to the Spleen.

Throughout its whole course, the pneumogastric contains both sensory and motor fibres; but after it has emerged from the skull, and, in some instances even sooner, it enters into so many anastomoses that it is hard to say whether the filaments it contains are, from their origin, its own, or whether they are derived from other nerves combining with it. This is particularly the case with the filaments of the sympathetic nerve, which are abundantly added to nearly all the branches of the pneumogastric. The likeness to the sympathetic which it thus acquires is further increased by its containing many filaments derived, not from the brain, but from its own petrosal ganglia, in which filaments originate, in the same manner as in the ganglia of the sympathetic, so abundantly that the trunk of the nerve is visibly larger below the ganglia than above them (Bidder and Volkmann). Next to the sympathetic nerve, that which most communicates with the pneumogastric is the accessory nerve, whose internal branch joins its trunk, and is lost in it.

The most probable account of the particular functions which the branches of the pneumogastric nerve discharge in the several parts to which they are distributed, may be drawn from Dr. John Reid's experiments on dogs. They show that,—1. The *pharyngeal* branch is the principal, if not the sole motor nerve of the pharynx and soft palate, and is most probably wholly motor; a part of its motor fibres being derived from the internal branch of the accessory nerve. 2. The *inferior* or *recurrent laryngeal* nerve is the motor nerve of the larynx. 3. The *superior laryngeal* nerve is chiefly sensory: the only muscle supplied by it being the crico-thyroid. 4. The motions of the *œsophagus* are dependent on motor fibres of the pneumogastric, and are probably excited by impressions made upon sensitive fibres of the same. 5. The *cardiac* branches of the pneumogastric nerve are one but not the sole channel through which the influence of the central organs and of mental emotions is transmitted to the heart. 6. The *pulmonary* branches form the principal but not the sole channel by which the impressions on the mucous surface of the lungs that excite respiration, are transmitted to the medulla oblongata.

Fig. 256.*



* Fig. 256. View of the nerves of the eighth pair, their distribution and connections on the left side (from Sappey after Hirschfeld and Leveillé). 1.— 1, pneumogastric nerve in the neck; 2, ganglion of its trunk; 3, its union with the spinal accessory; 4, its union with the hypoglossal; 5, pharyngeal branch; 6, superior laryngeal nerve; 7, external laryngeal; 8, laryngeal plexus; 9, inferior or recurrent laryngeal; 10, superior cardiac branch; 11, middle cardiac; 12, plexiform part of the nerve in the thorax; 13, posterior pulmonary plexus; 14, lingual or gustatory nerve of the inferior maxillary; 15, hypoglossal, passing into the muscles of the tongue, giving its thyro-hyoid branch, and uniting with twigs of the lingual; 16, glosso-pharyngeal nerve; 17, spinal accessory nerve, uniting by its inner branch with the pneumogastric,

The effects of section of the pneumogastric nerves have been made the subject of numerous experiments.

Division of both pneumogastric trunks, or of both their recurrent branches, is often very quickly fatal in young animals; but in old animals the division of the recurrent nerve is not generally fatal, and that of both the pneumogastric trunks is not always fatal (J. Reid), and, when it is so, the death ensues slowly. This difference is, probably, because the yielding of the cartilages of the larynx in young animals permits the glottis to be closed by the atmospheric pressure in inspiration, and they are thus quickly suffocated unless tracheotomy be performed (Legallois). In old animals, the rigidity and prominence of the arytenoid cartilages prevent the glottis from being completely closed by the atmospheric pressure; even when all the muscles are paralysed, a portion at its posterior part remains open, and through this the animal continues to breathe.

In the case of slower death, after division of both the pneumogastric nerves, the lungs are commonly found gorged with blood, œdematous, or nearly solid, or with a kind of low pneumonia, and with their bronchial tubes full of frothy bloody fluid and mucus, changes to which, in general, the death may be proximately ascribed. These changes are due, perhaps in part, to the influence which the pneumogastric nerves exercise on the movements of the air-cells and bronchi; yet, since they are not always produced in one lung when its pneumogastric nerve is divided, they cannot be ascribed wholly to the suspension of organic nervous influence (J. Reid). Rather, they may be ascribed to the hindrance to the passage of blood through the lungs, in consequence of the diminished supply of air and the excess of carbonic acid in the air-cells and in the pulmonary capillaries; in part, perhaps, to paralysis of the blood-vessels, leading to congestion; and in part, also, as the experiments of Traube especially show, they appear due to the passage of food and of the various secretions of the mouth and fauces through the glottis, which, being deprived of its sensibility, is no longer stimulated or closed in consequence of their contact. He says, that if the trachea be divided and separated from the œsophagus, or if only the œsophagus be tied, so that no food or secretion from above can pass down the trachea, no degeneration of the tissue of the lungs will follow the division of the pneumogastric nerves.

Regarding the influence of the pneumogastric nerve, see also Heart (p. 167), Arteries (p. 190), Glottis (p. 236), Larynx (p. 615), Trachea and Bronchi (p. 241), Lungs (p. 257-8), Pharynx and Œsophagus (p. 295), Stomach (p. 318), Liver (p. 360).

Spinal Accessory Nerve.—The principal branch of the accessory nerve, its external branch, supplies the sterno-mastoid and tra-

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and by its outer, passing into the sterno-mastoid muscle; 18, second cervical nerve; 19, third; 20, fourth; 21, origin of the phrenic nerve, 22, 23, fifth, sixth, seventh, and eighth cervical nerves, forming with the first dorsal the brachial plexus; 24, superior cervical ganglion of the sympathetic; 25, middle cervical ganglion; 26, inferior cervical ganglion united with the first dorsal ganglion; 27, 28, 29, 30, second, third, fourth, and fifth dorsal ganglia.

pezius muscles; and, though pain is produced by irritating it, is composed almost exclusively of motor fibres. It is very probable that the accessory nerve gives some motor filaments to the pneumogastric. For, among the experiments made on this point, many have shown that when the accessory nerve is irritated within the skull, convulsive movements ensue in some of the muscles of the larynx; all of which, as already stated, are supplied, apparently, by branches of the pneumogastric; and (which is a very significant fact) Vrolik states that in the chimpanzee the internal branch of the accessory does not join the pneumogastric at all, but goes direct to the larynx.

Among the roots of the accessory nerve, the lower, arising from the spinal cord, appear to be composed exclusively of motor fibres, and to be destined entirely to the trapezius and sterno-mastoid muscles; the upper fibres, arising from the medulla oblongata, contain many sensory as well as motor fibres.

Hypoglossal Nerve.—The hypoglossal or ninth nerve, or *motor linguæ*, has a peculiar relation to the muscles connected with the hyoid bone, including those of the tongue. It supplies through its descending branch (*descendens noni*), the sterno-hyoid, sterno-thyroid, and omo-hyoid; through a special branch the thyro-hyoid, and through its lingual branches the genio-hyoid, stylo-glossus, hyo-glossus, and genio-hyo-glossus and linguales. It contributes, also, to the supply of the submaxillary gland.

The function of the hypoglossal is exclusively motor, except in so far as its descending branch may receive a few sensory filaments from the first cervical nerve. As a motor nerve, its influence on all the muscles enumerated above is shown by their convulsions when it is irritated, and by their loss of power when it is paralysed. The effects of the paralysis of one hypoglossal nerve are, however, not very striking in the tongue. Often, in cases of hemiplegia involving the functions of the hypoglossal nerve, it is not possible to observe any deviation in the direction of the protruded tongue; probably because the tongue is so compact and firm that the muscles on either side, their insertion being nearly parallel to the median line, can push it straight forwards or turn it for some distance towards either side.

Physiology of the Spinal Nerves.

Little need be added to what has been already said of these nerves (pp. 509 to 520). The anterior roots of the spinal nerves are formed exclusively of motor fibres; the posterior roots exclusively of sensory fibres.

Beyond the ganglia, all the spinal nerves are mixed nerves, and contain as well sympathetic filaments.

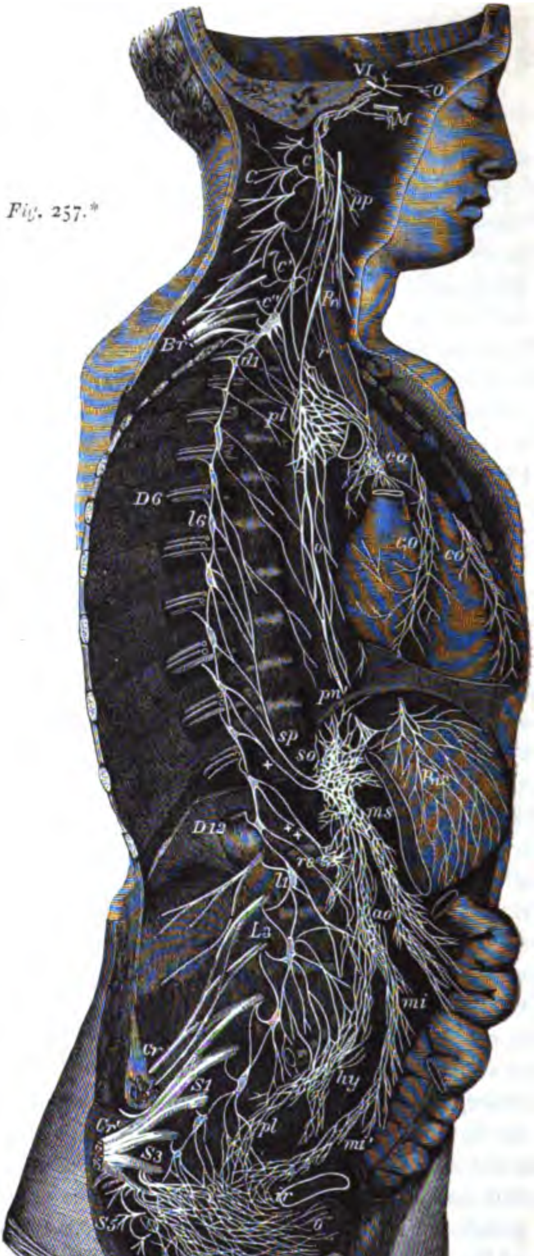
Of the functions of the ganglia of the spinal nerves nothing very definite is known. That they are not the reflectors of any of the ascertained reflex actions through the spinal nerves, is shown by the reflex movements ceasing when the posterior roots are divided between the ganglia and the spinal cord.

PHYSIOLOGY OF THE SYMPATHETIC NERVE.

The Sympathetic nerve, or Sympathetic system of nerves, obtained its name from the opinion that it is the means through which are effected the several sympathies in morbid action which distant organs manifest. It has also been called the *nervous system of organic life*, upon the supposition, now proved erroneous, that it alone, as a nervous system, influences the organic processes. Both terms are defective; but, since the title *sympathetic nerve* has the advantage of long and most general custom in its favour, and is not more inaccurate than the other, it will be here employed.

The general differences between the fibres of the cerebro-spinal and sympathetic nerves have been already stated (pp. 482-3); and it has been said, that although such general differences exist, and are sufficiently discernible in selected filaments of each system of nerves, yet they are neither so constant, nor of such a kind, as to warrant the supposition, that the different modes of action of the two systems can be referred to the different structures of their fibres. Rather, it is probable, that the laws of conduction by the fibres are in both systems the same, and that the differences manifest in the modes of action of the systems are due to the multiplication and separation of the nervous centres of the sympathetic: ganglia, or nerve-centres, being placed in connection with the fibres of the sympathetic in nearly all parts of their course.

Fig. 257.*



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* Fig. 257. Diagrammatic view of the Sympathetic cord of the right side, showing its connections with the principal cerebro-spinal nerves and the main præaortic plexuses. ⅕. (From Quain's Anatomy.)

Cerebro-spinal nerves.—VI, a portion of the sixth cranial nerve as it passes through the cavernous sinus, receiving two twigs from the carotid plexus of the sympathetic nerve; O, ophthalmic ganglion connected by a twig with the carotid plexus; M, connection of the spheno-palatine ganglion by the Vidian nerve with the carotid plexus; C, cervical plexus; Br, brachial plexus; D 6, sixth intercostal nerve; D 12, twelfth; L 3, third lumbar nerve; S 1, first sacral nerve; S 3, third; S 5, fifth; Cr, anterior crural nerve; Cr', great sciatic; *pn*, pneumo-gastric nerve in the lower part of the neck; *r*, recurrent nerve winding round the subclavian artery.

Sympathetic Cord.—*c*, superior cervical ganglion; *c'*, second or middle; *c"*, inferior: from each of these ganglia cardiac nerves (all deep on this side) are seen descending to the cardiac plexus; *d* 1, placed immediately below the first dorsal sympathetic ganglion; *d* 6, is opposite the sixth; *l* 1, first lumber ganglion; *c g*, the terminal or coccygeal ganglion.

Præaortic and Visceral Plexuses.—*p p*, pharyngeal, and, lower down, laryngeal plexus; *pl*, posterior pulmonary plexus spreading from the pneumogastric on the back of the right bronchus; *c a*, on the aorta, the cardiac plexus, towards which, in addition to the cardiac nerves from the three cervical sympathetic ganglia, other branches are seen descending from the pneumo-gastric and recurrent nerves; *co*, right or posterior, and *co'*, left or anterior coronary plexus; *o*, œsophageal plexus in long meshes on the gullet; *sp*, great splanchnic nerve formed by branches from the fifth, sixth, seventh, eighth, and ninth dorsal ganglia; +, small splanchnic from the ninth and tenth; + +, smallest or third splanchnic from the eleventh: the first and second of these are shown joining the solar plexus, *so*; the third descending to the renal plexus, *re*; connecting branches between the solar plexus and the pneumo-gastric nerves are also represented; *pn'*, above the place where the right pneumo-gastric passes to the lower or posterior surface of the stomach; *pn"*, the left distributed on the anterior or upper surface of the cardiac portion of the organ: from the solar plexus large branches are seen surrounding the arteries of the cœliac axis, and descending to *m s*, the superior mesenteric plexus; opposite to this is an indication of the suprarenal plexus; below *re* (the renal plexus), the spermatic plexus is also indicated; *a o*, on the front of the aorta, marks the aortic plexus, formed by nerves descending from the solar and superior mesenteric plexuses and from the lumbar ganglia; *mi*, the inferior mesenteric plexus surrounding the corresponding artery; *hy*, hypogastric plexus placed between the common iliac vessels, connected above with the aortic plexus, receiving nerves from the lower lumbar ganglia, and dividing below into the right and left pelvic or inferior hypogastric plexuses; *p l*, the right pelvic plexus; from this the nerves descending are joined by those from the plexus on the superior hemorrhoidal vessels, *mi'*, by sympathetic nerves from the sacral ganglia, and by numerous visceral nerves from the third and fourth sacral spinal nerves, and there are thus formed the rectal, vesical, and other plexuses, which ramify upon the viscera from behind forwards and from below upwards, as towards *ir*, and *v*, the rectum and bladder.

(For the general anatomical position and arrangement of the sympathetic nervous system, see p. 478 and fig. 257).

The special distribution of the fibres of the Sympathetic system is as follows:—

1. Fibres are distributed to all plain or unstriped muscular fibres, as those of the blood-vessels (vaso-motor nerves), of the muscular coats of the intestines and other hollow viscera, of gland-ducts, of the interior of the eyeball, and elsewhere.

The vaso-motor fibres come originally from the *vaso-motor centre* in the medulla oblongata; and, issuing from the spinal cord, communicate with the præ-vertebral chain of ganglia, and are thence, as branches from these, distributed to the blood-vessels.

2. Fibres (accelerating) are distributed to the Heart.

3. Secretory fibres (in addition to vaso-motor?) are distributed to the salivary, and presumably to other secreting glands.

4. Inter-central or inter-ganglionic fibres.

5. *Centripetal* fibres proceeding to the vaso-motor centre in the medulla; to the various sympathetic ganglia; and probably to all cerebro-spinal nerve-centres.

The *peripheral* distribution of these centripetal fibres is, without doubt, chiefly in the parts or organs to which the *centrifugal* fibres of the same system are mainly distributed. But they are also present in all those other parts of the body which belong more especially to the Cerebro-spinal system.

The structure of all the sympathetic ganglia appears to be essentially similar; all containing—(1), nerve-fibres traversing them; (2), nerve-fibres originating in them; (3), nerve- or ganglion-corpuscles, giving origin to these fibres; and (4), other corpuscles that appear free.

In the sympathetic ganglia of the frog, ganglion-cells of a very complicated structure have been described by Beale and subsequently by Arnold. The cells are enclosed each in a nucleated capsule: they are pyriform in shape, and from the pointed end two fibres are given off, which gradually acquire the characters of nerve-fibres: one of them is straight, and the other (which sometimes arises from the cell by two roots) is spirally coiled around it.

In the trunk, and thence proceeding branches of the sympathetic, there appear to be always—(1), fibres which arise in its

own ganglia; (2), fibres derived from the ganglia of the cerebral and spinal nerves; (3), fibres derived from the brain and spinal cord and transmitted through the roots of their nerves. The spinal cord, indeed, appears to be a large source of the fibres of the sympathetic nerve.

Through the communicating branches between the spinal nerves and the præ-vertebral sympathetic ganglia, which have been generally called roots or origins of the sympathetic nerve, an interchange is effected between all the spinal nerves and the sympathetic trunks; all the ganglia, also, which are seated on the cerebral nerves, have roots (as they are called) through which filaments of the cerebral nerves are added to their own. So that, probably, all sympathetic nerves contain some intermingled cerebral or spinal nerve-fibres; and all cerebral and spinal nerves some filaments derived from the sympathetic system or from ganglia. But the proportions in which these filaments are mingled are not uniform. The nerves which arise from the brain and spinal cord retain throughout their course and distribution a preponderance of *cerebro-spinal* fibres, while the nerves immediately arising from the so-called sympathetic ganglia probably contain a majority of *sympathetic* fibres. But inasmuch as there is no certainty that in structure the branches of cerebral or spinal nerves differ always from those of the sympathetic system, it is impossible in the present state of our knowledge to be sure of the source of fibres which from their structure might lead the observer to believe that they arose from the brain or spinal cord on the one hand, or from the sympathetic ganglia on the other. In other words, although the large white medullated fibres are especially characteristic of cerebro-spinal nerves, and the pale or non-medullated fibres of a sympathetic nerve, in which they largely preponderate, there is no certainty to be obtained in a doubtful case, of whether the nerve-fibre is derived from one or the other, from mere examination of its structure. It may be derived from either source.

Functions of the Sympathetic Nervous System.

With respect to the functions of the Sympathetic nervous system, it may be stated generally that the sympathetic nerve-fibres are simple conductors of impressions, as those of the Cerebro-spinal system are; and that the ganglionic centres have (each in its appropriate sphere) the like powers both of *conducting*, *transferring*, and *reflecting* impressions made on them.

The power possessed by the sympathetic ganglia of conducting impressions is sufficiently proved in disease, as when any of the viscera, usually unfelt, give rise to sensations of pain, or when a part not commonly subject to mental influence is excited or retarded in its actions by the various conditions of the mind; for in all these cases impressions must be conducted to and fro

through the whole distance between the part and the spinal cord and brain. So, also, in experiments, now more than sufficiently numerous, irritations of the semilunar ganglia, the splanchnic nerves, the thoracic, hepatic, and other ganglia and nerves, have elicited expressions of pain, and have excited movements in the muscular organs supplied from the irritated part.

In the case of pain, or of movements affected by mental conditions, it may be supposed that the conduction of impressions is effected through the cerebro-spinal fibres which are mingled in all, or nearly all, parts of the sympathetic nerves. There are no means of deciding this; but if it be admitted that the conduction is effected through the cerebro-spinal nerve-fibres, then, whether or not they pass uninterruptedly between the brain or spinal cord and the part affected, it must be assumed that their mode of conduction is modified by the ganglia. For, if such cerebro-spinal fibres are conducted in the ordinary manner, the parts should be always sensible and liable to the influence of the will, and impressions should be conveyed to and fro instantaneously. But this is not the case; on the contrary, through the branches of the sympathetic nerve and its ganglia, none but intense impressions, or impressions exaggerated by the morbid excitability of the nerves or ganglia, can be conveyed.

Respecting the general action of the ganglia of the sympathetic nerve, in reflex or other actions, little need be said here, since they may be taken as examples by which to illustrate the common modes of action of all nerve-centres (see p. 496). Indeed, complex as the sympathetic system, taken as a whole, is, it presents in each of its parts a simplicity not to be found in the cerebro-spinal system: for each ganglion with afferent and efferent nerves forms a simple nervous system, and might serve for the illustration of all the nervous actions with which the mind is unconnected.

The parts principally supplied with sympathetic nerves are usually capable of none but involuntary movements, and when the mind acts on them at all, it is only through the strong excitement or depressing influence of some passion, or through some voluntary movement with which the actions of the involuntary

part are commonly associated. The heart, stomach, and intestines are examples of these statements; for the heart and stomach, though supplied in large measure from the pneumogastric nerves, yet probably derive through them few filaments except such as have arisen from their ganglia, and are therefore of the nature of sympathetic fibres.

The parts which are supplied with motor power by the sympathetic nerve continue to move, though more feebly than before, when they are separated from their natural connections with the rest of the sympathetic system, and wholly removed from the body. Thus, the heart, after it is taken from the body, continues to beat in Mammalia for one or two minutes, in reptiles and Amphibia for hours; and the peristaltic motions of the intestine continue under the same circumstances. Hence the motion of the parts supplied with nerves from the sympathetic are shown to be, in a measure, independent of the brain and spinal cord; this independent maintenance of their action being, without doubt, due to the fact that they contain, in their own substance, the apparatus of ganglia and nerve-fibres by which their motions are immediately governed.

It seems to be a general rule, at least in animals that have both cerebro-spinal and sympathetic nerves much developed, that the involuntary movements excited by stimuli conveyed through ganglia are orderly and like natural movements, while those excited through nerves without ganglia are convulsive and disorderly; and the probability is that, in the natural state, it is through the same ganglia that natural stimuli, impressing centripetal nerves, are reflected through centrifugal nerves to the involuntary muscles. As the muscles of respiration are maintained in uniform rhythmic action chiefly by the reflecting and combining power of the medulla oblongata, so are those of the heart, stomach, and intestines, by their several ganglia. And as with the ganglia of the sympathetic and their nerves, so with the medulla oblongata and its nerves distributed to the respiratory muscles,—if these nerves of the medulla oblongata itself be directly stimulated, the movements that follow are convulsive and disorderly; but if the medulla be stimulated through a

centripetal nerve, as when cold is applied to the skin, then the impressions are reflected so as to produce movements which, though they may be very quick and almost convulsive, are yet combined in the plan of the proper respiratory acts.

Among the ganglia of the sympathetic nerves to which this co-ordination of movements is to be ascribed, must be reckoned, not those alone which are on the principal trunks and branches of the sympathetic external to any organ, but those also which lie in the very substance of the organs; such as those of the heart (p. 164). Those also may be included which have been found in the mesentery close by the intestines, as well as in the muscular and sub-mucous tissue of the stomach and intestinal canal (p. 323), and in other parts. The extension of discoveries of such ganglia will probably diminish yet further the number of instances in which the involuntary movements appear to be effected independently of nervous influence.

Respecting the influence of the sympathetic system on various physiological processes, see Heart (p. 167), Arteries (p. 188), Animal Heat (p. 273), Salivary Glands (p. 289), Stomach (p. 318), Intestines (p. 369), Liver (p. 360), Nutrition (p. 403). These are parts which have been specially investigated. But they are not in any way exceptional. All physiological processes must, of necessity, either directly or through vaso-motor fibres, be under the influence of the Sympathetic system.

It is, of course, very difficult to determine the relative share exercised by the sympathetic and the cerebro-spinal fibres in these various processes, since both kinds of fibres appear to be distributed to most parts, and there seems to be no possibility of isolating them. Probably the safest view of the question at present is, still to regard all the processes of organic life, in man, as liable to the combined influences of the cerebro-spinal and the sympathetic systems; to consider that those influences may be so combined as that the sympathetic nerves and ganglia may be in man, as in the lower animals, the parts through which the ordinary and constant influence of nervous force is exercised on the organic processes; while the cerebro-spinal nervous centres and their ganglia are so closely connected with

the proper sympathetic ganglia, that neither of them can be said to be independent of the other; each, as a rule, and under ordinary circumstances, governing its own domain, but always liable to be influenced by the other.

CHAPTER XIX.

CAUSES AND PHENOMENA OF MOTION.

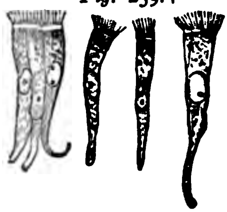
In the animal body, motion is produced in these several ways. (1). The oscillatory or vibratory movement of *Cilia*. (2). *Amœboid* and certain *Molecular* movements. (3). The contraction of *Muscular fibre*.

CILIARY MOTION.

Ciliary, which is closely allied to amœboid and muscular motion (p. 583) consists in the incessant vibration of fine, pellucid processes, about $\frac{1}{5000}$ of an inch long, termed *cilia* (figs. 258, 259), situated on the free extremities of the cells of epithelium covering certain surfaces of the body.

Fig. 258.*

Fig. 259.†



The distribution and structure of ciliary epithelium and the microscopic appearances of cilia in motion have been already described (p. 66).

Ciliary motion is alike independent of the will, of the direct influence of the nervous system, and of muscular contraction. It continues for several hours after death or removal from the body,

* Fig. 258. Spheroidal ciliated cells from the mouth of the frog; magnified 300 diameters (Sharpey).

† Fig. 259. Columnar ciliated epithelium-cells from the human nasal membrane; magnified 300 diameters (Sharpey).

provided the portion of tissue under examination be kept moist. Its independence of the nervous system is shown also in its occurrence in the lowest invertebrate animals apparently unprovided with anything analogous to a nervous system, in its persistence in animals killed by prussic acid, by narcotic or other poisons, and after the direct application of narcotics to the ciliary surface, or the discharge of a Leyden jar, or of a galvanic shock through it. The vapour of chloroform arrests the motion; but it is renewed on the discontinuance of the application (Lister). According to Kühne, the movement ceases in an atmosphere deprived of oxygen, but is revived on the admission of this gas. Carbonic acid stops the movement. The contact of various substances will stop the motion altogether; but this seems to depend chiefly on destruction of the delicate substance of which the cilia are composed.

Little or nothing is known with certainty regarding the nature of ciliary action. As Dr. Sharpey observes, however, it is a special manifestation of a similar property to that by which the other motions of animals are effected, namely, by what we term *vital contractility*. The fact of the more evident movements of the larger animals being effected by a structure apparently different from that of cilia, is no argument against such a supposition. For, if we consider the matter, it will be plain that our prejudices against admitting a relationship to exist between the two structures, muscles and cilia, rests on no definite ground; and for the simple reason, that we know so little of the manner of production of movement in either case. The mere difference of structure is not an argument in point; neither is the presence or absence of nerves. For in the fœtus the heart begins to pulsate when it consists of a mass of embryonic cells, and long before either muscular or nervous tissue has been differentiated. The movements of both muscles and cilia are manifestations of *energy*, by certain special structures, which we call respectively muscles and cilia. We know nothing more about the means by which the manifestation is effected by one of these structures than by the other; and the mere fact that one has nerves and the other has not, is no more argument against cilia having what we call a vital power of contraction, than the presence or absence of stripes from voluntary or involuntary muscles respectively, is an argument for or against the contraction of one of them being vital and the other not so. Inasmuch then as cilia are found in living structures only, and inasmuch as they are a means whereby energy is transformed (see Chap. II.), their peculiar properties have as much right to be invested with the term *vital* as have those of muscular fibres. The term may be in both instances a bad one,—it certainly is an unsatisfactory one,—but it is as good for one case as the other.

As a special subdivision of ciliary action may be mentioned

the motion of spermatozoa, which may be regarded as cells with a single cilium. (See Chapter on Generation.)

AMŒBOID MOTION.

The remarkable movements observed in colourless blood-corpuscles, connective-tissue corpuscles, and many other cells (p. 46) must be regarded as depending on a kind of contraction of portions of their mass very similar to muscular contraction.

There is certainly an analogy between the spherical form assumed by a colourless blood corpuscle on electric stimulation and the condition known as tetanus in muscles.

MUSCULAR MOTION.

There are two chief kinds of muscular tissue, the *striated*, and the *plain* or *non-striated*, and they are distinguished by structural peculiarities and mode of action. The striped form of muscular fibre is sometimes called *voluntary* muscle, because all muscles under the control of the will are constructed of it. The plain or unstriped variety is often termed *involuntary*, because it alone is found in the greater number of the muscles over which the will has no power.

Plain or Non-striated Muscles.

The non-striated Muscles are made up (Kölliker), of elongated, spindle-shaped, nucleated *fibre cells* (fig. 260), which in their perfect form are flat, from about $\frac{1}{4500}$ to $\frac{1}{3500}$ of an inch broad, and $\frac{1}{600}$ to $\frac{1}{300}$ of an inch in lengh,—very clear, granular, and brittle, so that when they break, they often have abruptly rounded or square extremities. Each fibre-cell possesses an elongated nucleus, and many are marked along the middle, or, more rarely, along one of the edges, either by a fine continuous dark streak, or by short isolated dark lines, or by dark points arranged in a row, or scattered. These fibre-cells, by their union, form *fibres* and bundles of fibres (fig. 261). The fibres have no distinct sheath.

The fibres of involuntary muscle, such as are here described, form the proper muscular coats of the digestive canal from the

middle of the œsophagus to the internal sphincter ani, of the ureters and urinary bladder, the trachea and bronchi, the ducts of glands, the gall-bladder, the vesiculæ seminales, the pregnant uterus, of blood-vessels and lymphatics, the iris, and some other parts.

Fig. 260.*

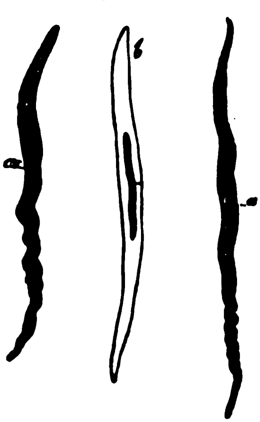


Fig. 261.†

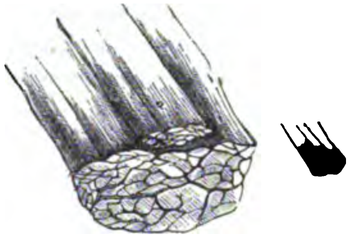
This form of tissue also enters largely into the composition of the tunica dartos, and is the principal cause of the wrinkling and contraction of the scrotum on exposure to cold. The fibres of the cremaster assist in some measure in producing this effect, but they are chiefly concerned in drawing up the testis and its coverings towards the inguinal opening. Unstriped muscular tissue occurs largely also in the cutis (p. 432), being especially abundant in the interspaces between the bases of the papillæ. Hence, when it contracts under the influence of cold, fear, electricity, or any other stimulus, the papillæ are made unusually prominent, and give rise to the peculiar roughness of the skin termed *cutis anserina*, or goose-skin. It occurs also in the superficial portion

* Fig. 260. Muscular fibre-cells from human arteries, magnified 350 diameters. *a*, natural state; *b*, treated with acetic acid (Kölliker).

† Fig. 261. Plain muscular fibres from the human bladder, magnified 250 diameters. *a*, in their natural state; *b*, treated with acetic acid to show the nuclei.

of the cutis, in all parts where hairs occur, in the form of flattened roundish bundles, which lie alongside the hair-follicles and sebaceous glands. They pass obliquely from without inwards, embrace the sebaceous glands, and are attached to the hair follicles near their base (fig. 262).

Fig. 262.* *Fig.* 263.†



Striated Muscles.—The striated muscles include the whole class of *voluntary* muscles, the *heart*, and those muscles neither completely voluntary nor involuntary, which form part of the walls of the pharynx, and exist in many other parts of the body, as the internal ear, urethra, etc. All these muscles are composed of fleshy bundles called *fasciculi*, enclosed in coverings of fibro-cellular tissue, by which each is at once connected with, and isolated from, those adjacent to it (fig. 263). Each bundle is again divided into smaller ones, similarly ensheathed and similarly divisible; and so on, through an uncertain number of gradations, till one arrives at the primitive fasciculi, or the muscular *fibres* properly so called.

Each muscular fibre is thus constructed:—Externally is a fine, transparent, structureless membrane, called the *sarcolemma*, which in the form of a tubular investing sheath forms the outer wall of the fibre, and is filled up by the contractile material of which the fibre is chiefly made up. Sometimes, from its

* Fig. 262. Perpendicular section through the scalp, with two hair-sacs; *a*, epidermis; *b*, cutis; *c*, muscles of the hair-follicles (Kölliker).

† Fig. 263. A small portion of muscle, natural size, consisting of larger and smaller fasciculi, seen in a transverse section, and the same magnified 5 diameters (Sharpey.)

comparative toughness, the sarcolemma will remain untorn, when by extension the contained part can be broken (fig. 264), and its presence is in this way best demonstrated. The fibres, which are cylindriform or prismatic, with an average diameter of about $\frac{1}{500}$ of an inch, are of a pale yellow colour, and apparently marked by fine striæ, which pass transversely round them, in slightly curved or wholly parallel lines. Other, but generally more obscure striæ, also pass longitudinally over the tubes, and indicate the direction of the filaments or primitive *fibrils* of which the substance of each *fibre* is composed (fig. 265).

Fig. 264.*

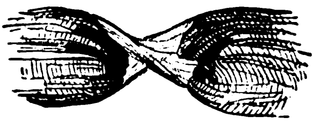
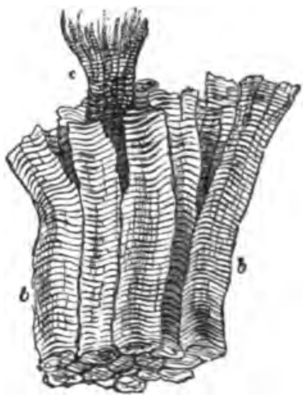


Fig. 265.†



The whole substance of the fibre contained within the sarcolemma may be thus supposed to be constructed of longitudinal fibrils—a bundle of *fibrils* surrounded by the sarcolemma constituting a *fibre*.

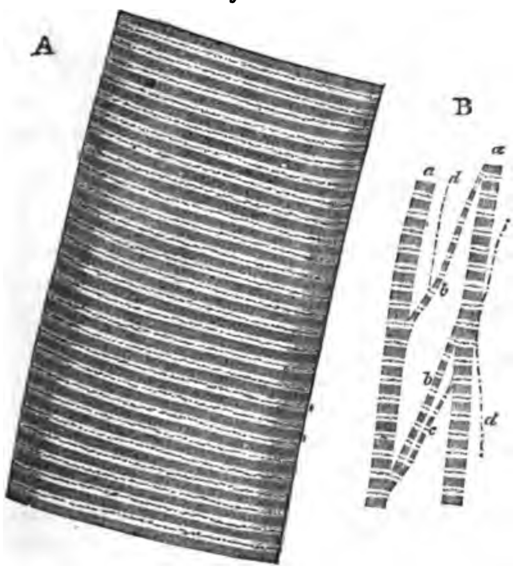
There is still some doubt regarding the nature of the fibrils. Each of them appears to be composed of a single row of minute dark quadrangular particles called *sarcous elements*, which are separated from each other by a bright space formed of a pellucid

* Fig. 264. Muscular fibre torn across; the sarcolemma still connecting the two parts of the fibre (Todd and Bowman).

† Fig. 265. A few muscular fibres, being part of a small fasciculus, highly magnified, showing the transverse striæ. *a*, end view of *b*, *b*, fibres; *c*, a fibre split into its fibrils (Sharpey).

substance continuous with them. Dr. Sharpey believes that, even in a fibril so constituted, the ultimate anatomical element of the fibre has not been isolated. He believes that each fibril with quadrangular sarcous elements is composed of a number of other fibrils still finer, so that the sarcous element of an ultimate fibril would be not quadrangular but as a streak. In either case the appearance of striation in the whole fibre would be produced by the arrangement, side by side, of the dark and light portions respectively of the fibrils (fig. 266).

Fig. 266.*

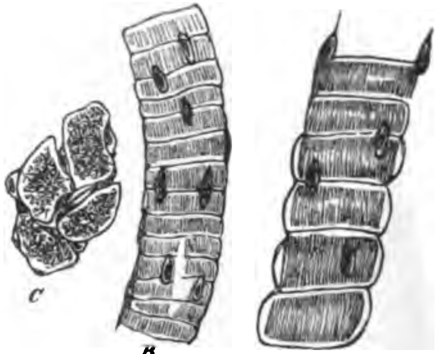


A fine streak can usually be discerned passing across the bright interval between the sarcous elements: this streak is termed Krause's membrane: it is continuous at each end with the sarcolemma investing the muscular fibre (fig. 267 *A*).

* Fig. 266. A. Portion of a medium-sized human muscular *fibre*, magnified nearly 800 diameters. B. Separated bundles of *fibrils* equally magnified; *a*, *a*, larger, and *b*, *b*, smaller collections; *c*, still smaller; *d*, *d*, the smallest which could be detached, possibly representing a single series of sarcous elements (Sharpey).

Thus the space enclosed by the sarcolemma is divided into a series of compartments by the transverse partitions, known as Krause's membranes; these compartments being occupied by the true muscle substance. On each side (above and below) of Krause's membrane is a bright border (lateral disc) which sometimes can be seen to contain a row of granules. In the centre of the dark zone of sarcous elements a lighter band can sometimes be dimly discerned: this is termed the middle disc of Hensen (see fig. 267).

Fig. 267.*



The sarcous elements and Krause's membranes are doubly refracting, the rest of the fibre singly refracting (Brücke).

According to Schäfer, the granules, which have been mentioned on either side of Krause's membrane, are little knobs attached to the ends of "muscle-rods;" and these muscle-rods, knobbed at each end and imbedded in a homogeneous protoplasmic ground-substance, form the substance of the muscles. This view, however, of the structure of muscle requires further confirmation before it can be finally accepted.

Although each muscular fibre may be considered to be formed of a number of longitudinal fibrils, arranged side by side, it is

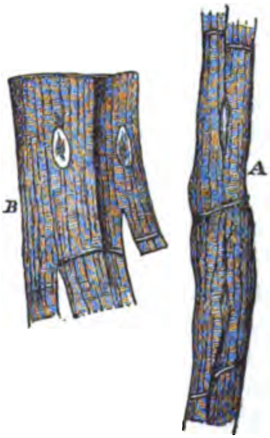
* Fig. 267. *A*, muscle-fibre of water-beetle (hydrophilus pisceus), semi-diagrammatic, showing the sarcolemma continuous with the "Krause's" membrane, which separates the sarcous elements. The bulging of the sarcolemma is a common appearance and is probably post mortem. The median disc of Hensen is dimly seen as a light transverse band in the centre of each dark band. *B*, muscle-fibre from the tongue, highly magnified; *C*, transverse section of a similar fibre, showing the position of the muscle nuclei (W. Pye).

also true that they are not naturally separate from each other, there being *lateral* cohesion, if not fusion, of each sarcous element with those around and in contact with it; so that it happens that there is a tendency for a fibre to split, not only into separate fibrils, but also occasionally into plates or disks, each of which is composed of sarcous elements laterally adherent one to another.

The muscular fibres of the heart form the chief, though not the only exception to the rule, that involuntary muscles are constructed of *plain* fibres; but although striated and so far resembling those of the voluntary muscles, they present these distinctions:—Each muscular fibre is made up of elongated, nucleated, and branched cells (fig. 269). The fibres are finer and less distinctly striated than those of the voluntary muscles; and no sarcolemma can be usually discerned.

Fig. 268.*

Fig. 269†



The voluntary muscles are freely supplied with blood-vessels; the capillaries form a network with oblong meshes around the

* Fig. 268. Muscular fibres from the heart, magnified, showing their cross-striæ, divisions, and junctions (Kölliker).

† Fig. 269. A. Muscular fibres from the heart of man, divided by transverse septa into separate nucleated portions. B. Two laterally adherent muscl -cells from the guinea-pig (Schweigger-Seidel).

fibres on the outside of the sarcolemma. No vessels penetrate the sarcolemma to enter the interior of the fibre.

Nerves also are supplied freely to muscles; the voluntary muscles receiving chiefly nerves from the cerebro-spinal system, and the unstriped muscles from the sympathetic or ganglionic system.

Development of Muscular Tissue.

Unstriped.—The cells of unstriped muscle are derived directly from embryonic cells, by an elongation of the cell, and its nucleus; the latter changing from a vesicular to a rod shape.

Striped.—Formerly it was supposed that striated fibres are formed by the coalescence of several cells, but recently it has been proved (Remak, Wilson Fox), that each fibre is formed from a single cell, the process involving an enormous increase in size, a multiplication of the nucleus by fission, and a differentiation of the cell-contents.

This view differs but little from that previously taken by Savory, viz., that the muscular fibre is produced not by multiplication of cells, but by arrangement of nuclei in a growing mass of protoplasm (answering to the cell in the theory just referred to), which becomes gradually differentiated so as to assume the characters of a fully developed muscular fibre.

Growth of Muscle.—The growth of muscles both striated and non-striated is the result of an increase both in the number and size of the individual elements.

In the pregnant uterus the fibre-cells may become enlarged to ten times their original length (Kölliker). In involution of the uterus after parturition the reverse changes occur, accompanied generally by some fatty infiltration of the tissue and degeneration of the fibres.

Chemical Constitution of Muscle.

Fresh muscle is neutral or slightly alkaline in reaction when at rest: when in a condition of activity or of rigor its reaction becomes distinctly acid.

Muscle, like blood, may be analysed into two parts by purely mechanical means. For this purpose the muscle-juice or *plasma*, as it may be termed, is obtained as follows: A portion of frogs,

muscle (after the blood has been completely expelled by the injection of a solution of common salt), is squeezed: the juice thus expressed is the muscle-*plasma;* or a portion of muscle may be frozen and then reduced to a pulp, mixed with salt solution and thrown upon a filter: the filtrate is muscle-*plasma.* It is a colourless somewhat turbid fluid, which can be coagulated by a temperature of 120° F., or by the action of acids.

By this coagulation a rough analysis of the muscle substance takes place just as in the case of the blood. The coagulum obtained is termed *myosin;* while the remaining watery fluid is called *muscle-serum.*

Myosin is an albuminoid body which is soluble in strong solutions of common salt, and also in dilute acids, by which it is converted into *syntonin* or *acid-albumin.* Muscle-serum contains a variety of substances in solution, among which the principal are albuminous bodies, fat, free acids, especially lactic, formic, and acetic, glycogen and inosite, kreatin, hypoxanthin, many salts, carbonic acid, and lastly hæmoglobin, on which the colour of muscles depends (p. 118).

Physiology of Muscle.

Muscle may exist in three different conditions; *rest, activity,* and *rigor.*

(1). *Rest.*—In this condition a muscle has a slight but very perfect elasticity; it admits of being considerably stretched; but returns readily and completely to its normal length.

In the living body the muscles are always stretched somewhat beyond their natural length, they are always in a condition of slight tension; an arrangement which enables the whole force of the contraction to be utilised in approximating the points of attachment. It is obvious that if the muscles were lax, the first part of the contraction till the muscle became tight would be wasted.

There is no doubt that even in a condition of rest oxygen is abstracted from the blood and carbonic acid given out by a muscle; for the blood becomes venous in the transit. When cut out of the body such muscles retain their contractility longer in an atmosphere of oxygen than in hydrogen or carbonic acid.

(2). *Activity.*—The property of muscular tissue, by which its peculiar functions are exercised, is its *contractility,* which is excited by all kinds of stimuli, applied either directly to the

muscles, or indirectly to them through the medium of their motor nerves. This property, although commonly brought into action through the nervous system, is inherent in the muscular tissue. For—(1). it may be manifested in a muscle which is isolated from the influence of the nervous system by division of the nerves supplying it, so long as the natural tissue of the muscle is duly nourished; and (2). it is manifest in a portion of muscular fibre, in which, under the microscope, no nerve-fibre can be traced. (3). Substances such as *curare*, which paralyse the nerve-endings in muscles, do not at all diminish the irritability of the muscle. (4). When a muscle is fatigued, a local stimulation is followed by a contraction of a small part of the fibre in the immediate vicinity without any regard to the distribution of nerve-fibres.

The stimuli which excite the contraction of muscles may be classed as follows: nerve currents, electric currents, chemical, thermal, and mechanical stimuli.

If the removal of nervous influence be long continued, as by division of the nerve supplying a muscle, or in cases of paralysis of long-standing, the irritability, *i.e.*, the power of both perceiving and responding to a stimulus, may be lost; but probably this is chiefly due to the impaired nutrition of the muscular tissue, which ensues through its inaction (J. Reid). The irritability of muscles is also of course soon lost, unless a supply of arterial blood to them is kept up. Thus, after ligature of the main arterial trunk of a limb, the power of moving the muscles is partially or wholly lost, until the collateral circulation is established; and when, in animals, the abdominal aorta is tied, the hind legs are rendered almost powerless (Segalas).

The same fact may be readily shown by compressing the abdominal aorta in a rabbit for about 10 min.; if the pressure be released and the animal be placed on the ground, it will work itself along with its front legs, while the hind legs sprawl helplessly behind. Gradually the muscles recover their power and become quite as efficient as before.

So, also, it is to the imperfect supply of arterial blood to the muscular tissue of the heart, that the cessation of the action of this organ in asphyxia is in some measure due (p. 261).

Besides the property of contractility, the muscles, especially the *striated*, possess sensibility by means of the sensory nerve-fibres distributed to them. The amount of common sensibility in muscles is not great; for they may be cut or pricked without giving rise to severe pain, at least in their healthy condition. But they have a peculiar sensibility, or at least a peculiar modification of common sensibility, which is shown in that their nerves can communicate to the mind an accurate knowledge of their states and positions when in action. By this sensibility, we are not only made conscious of the morbid sensations of fatigue and cramp in muscles, but acquire, through muscular action, a knowledge of the distance of bodies and their relation to each other, and are enabled to estimate and compare their weight and resistance by the effort of which we are conscious in measuring, moving, or raising them. Except with such knowledge of the position and state of each muscle, we could not tell how or when to move it for any required action; nor without such a sensation of effort could we maintain the muscles in contraction for any prolonged exertion.

The following are the leading facts which have been ascertained by experiment with regard to the conditions of muscular action and the tissue changes involved in the process.

(*a*) The irritability of muscle is greatest at a certain mean temperature; (*b*) after a number of contractions a muscle gradually becomes exhausted; (*c*) the activity of muscles after a time disappears altogether when they are removed from the body or the arteries are tied; (*d*) oxygen is used up in muscular contraction, but a muscle will act for a time in vacuo or a gas which contains no oxygen: in this case it is of course using up the oxygen already in store (Hermann); (*e*) the reaction of a muscle becomes acid during contraction; (*f*) it is exceedingly probable that during muscular activity the myosin undergoes some chemical transformation, but it is important to note that only a very slight increase of nitrogenous waste, as measured by the amount of urea excreted, results from muscular action. The muscle is enabled to maintain its activity by the constant supply

of oxygen, and some as yet unknown non-nitrogenous body, together with the continual removal of the waste products.

The *mode of contraction* in the transversely-striated muscular tissue, has been much disputed. The most probable account, which has been especially illustrated by Mr. Bowman, is that the contraction is effected by an approximation of the constituent parts of the fibrils, which, at the instant of contraction, without any alteration in their general direction, become closer, flatter, and wider; a condition which is rendered evident by the approximation of the transverse striæ seen on the surface of the fasciculus, and by its increased breadth and thickness. The appearance of the zigzag lines into which it was supposed the fibres are thrown in contraction, is due to the relaxation of a fibre which has been recently contracted, and is not at once stretched again by some antagonist fibre, or whose extremities are kept close together by the contractions of other fibres. The contraction is therefore a simple, and, according to Ed. Weber, an uniform, simultaneous, and steady shortening of each fibre and its contents. What each fibril or fibre loses in length, it gains in thickness: the contraction is a change of form not of size; it is, therefore, not attended with any diminution in bulk, from condensation of the tissue. This has been proved for entire muscles, by making a mass of muscle, or many fibres together, contract in a vessel full of water, with which a fine, perpendicular, graduated tube communicates. Any diminution of the bulk of the contracting muscle would be attended by a fall of fluid in the tube; but when the experiment is carefully performed, the level of the water in the tube remains the same, whether the muscle be contracted or not.

Edward Weber, however, states that a very slight diminution does take place in the bulk of a contracting muscle; but it is so slight as to be practically of no moment.

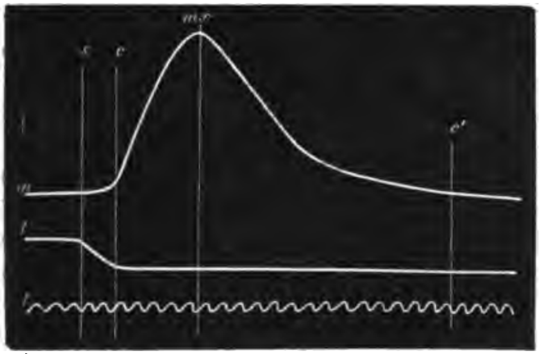
In thus shortening, muscles appear to swell up, becoming rounder, more prominent, harder, and apparently tougher. But this hardness of muscle in the state of contraction, is not due to increased firmness or condensation of the muscular tissue, but to the increased tension to which the fibres, as well as their

tendons and other tissues, are subjected from the resistance ordinarily opposed to their contraction. When no resistance is offered, as when a muscle is cut off from its tendon, not only is no hardness perceived during contraction, but the muscular tissue is even softer, more extensile, and less elastic than in its ordinary uncontracted state (Ed. Weber).

By the use of a recording instrument (myographion) similar in principle to the kymographion (p. 185) the process of contraction has been accurately studied.

The accompanying diagram (fig. 270) represents a muscle-curve traced on a revolving cylinder, by a weighted lever to which a muscle is attached.

Fig. 270.*



The upper line (*m*) represents the curve traced by the end of the lever after stimulation of the muscle by a single induction-shock: the middle line (*l*) is that described by the marking-lever, and indicates by a sudden drop the exact instant at which the induction-shock was given. The lower wavy line (*t*) is traced by a vibrating tuning-fork, and serves to measure precisely the intervals of time occupied in each part of the contraction.

It will be observed that after the stimulus has been applied, as indicated by the vertical line *s*, there is an interval before the contraction commences, as indicated by the line *c*. This interval, termed the "*latent period*" (Helmholtz), when measured by the

* Fig. 270. Muscle-curve (Michael Foster). (For explanation, *see* text.)

number of vibrations of the tuning-fork between the lines *s* and *c*, is found to be about $\frac{1}{100}$ sec.

The contraction progresses rapidly at first and afterwards more slowly to the maximum (the point in the curve through which the line *mx* is drawn), and then the muscle elongates again as indicated by the descending curve, at first rapidly, afterwards more slowly, till it attains its original length at the point indicated by the line *c'*.

The muscle curve obtained from the heart resembles that of unstriped muscles in the long duration of the effect of stimulation; the descending curve is very much prolonged.

The *force* of a muscle progressively diminishes during contraction. Thus, if a muscle can just raise a given weight at the commencement of contraction, it will be quite unable to raise it, if the weight does not come into play till near the end of contraction.

Work done by Muscles.

We have seen (p. 163) that *work* is estimated by multiplying the weight raised, by the height through which it has been lifted. It has been found that in order to obtain the maximum of work, a muscle must be moderately loaded: if the weight be increased beyond a certain point, the muscle becomes strained and raises the weight through so small a distance that less work is accomplished. If the load is still further increased the muscle is completely overtaxed, cannot raise the weight, and consequently does no work at all. Practical illustrations of these facts must be familiar to every one.

The power of a muscle is usually measured by the maximum weight which it will support without stretching. In man this is readily determined by weighting the body to such an extent that it can no longer be raised on tiptoe: thus the power of the calf-muscles is determined. (Weber).

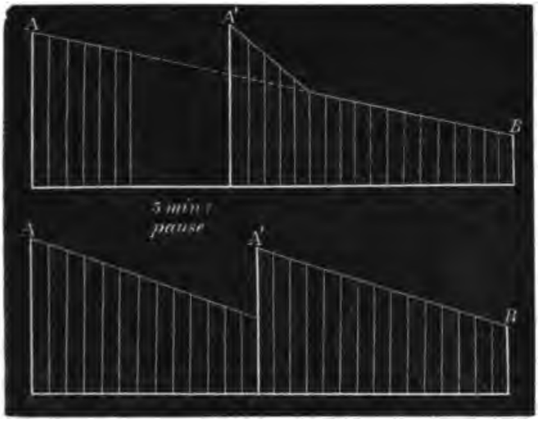
The power of a muscle thus estimated depends of course upon its cross-section. The power of a human muscle is from two to three times as great as a frog's muscle of the same sectional area.

Fatigue of Muscle.—A muscle becomes rapidly exhausted from

repeated stimulation, and the more rapidly, the more quickly the induction shocks succeed each other.

This is indicated by the diminished height of contraction in the accompanying diagrams (fig. 271). It will be seen that the vertical lines, which indicate the extent of the muscular contraction, decrease in length from left to right. The line A B drawn along the tops of these lines is termed the "fatigue curve." It is usually a straight line.

Fig. 271.*



In the first diagram the effects of a short rest are shown: there is a pause of three minutes, and when the muscle is again stimulated it contracts up to A', but the recovery is only temporary, and the *fatigue curve*, after a few more contractions, becomes continuous with that before the rest.

In the second diagram is represented the effect of a stream of oxygenated blood. Here we have a sudden restoration of energy: the muscle in this case makes an entirely fresh start from A, and the new fatigue curve is parallel to, and never coincides with the old one.

A fatigued muscle has a much longer "latent period" than a

Fig. 271. Fatigue-curves of muscle (Ray Lankester). (For explanation, *see* text.)

fresh one. The slowness with which muscles respond to the will when fatigued must be familiar to every one.

In a muscle which is exhausted, stimulation only causes a contraction producing a local bulging near the point irritated. A similar effect may be produced in a fresh muscle by a sharp blow, as in striking the biceps smartly with the edge of the hand, when a hard muscular swelling is instantly formed.

Heat is developed in the contraction of muscles. Becquerel and Breschet found, with the thermo-multiplier, about 1° of heat produced by each forcible contraction of a man's biceps; and when the actions were long continued, the temperature of the muscle increased 2°. It is not known whether this development of heat is due to chemical changes ensuing in the muscle, or to the friction of its fibres vigorously acting: in either case, we may refer to it a part of the heat developed in active exercise (p. 264).

Sound is said to be produced when muscles contract forcibly. Dr. Wollaston showed that this sound might be easily heard by placing the tip of the little finger in the ear, and then making some muscles contract, as those of the ball of the thumb, whose sound may be conducted to the ear through the substance of the hand and finger. A low shaking or rumbling sound is heard, the height and loudness of the note being in direct proportion to the force and quickness of the muscular action, and to the number of fibres that act together, or, as it were, in time.

The two kinds of fibres, the striped and unstriped, have characteristic differences in the mode in which they act on the application of the same stimulus; differences which may be ascribed in great part to their respective differences of structure, but to some degree, possibly, to their respective modes of connection with the nervous system. When irritation is applied directly to a muscle with striated fibres, or to the motor nerve supplying it, contraction of the part irritated, and of that only, ensues; and this contraction is instantaneous, and ceases on the instant of withdrawing the irritation. But when any part with unstriped muscular fibres, *e.g.*, the intestines or bladder, is irritated, the subsequent contraction ensues more slowly, extends

beyond the part irritated, and, with alternating relaxation, continues for some time after the withdrawal of the irritation. Ed. Weber particularly illustrated the difference in the modes of contraction of the two kinds of muscular fibres by the effects of the electro-magnetic stimulus. The rapidly succeeding shocks given by this means to the nerves of muscles excite in all the transversely-striated muscles a fixed state of tetanic contraction, which lasts as long as the stimulus is continued, and on its withdrawal instantly ceases: but in the muscles with smooth fibres they excite, if any movement, only one that ensues slowly, is comparatively slight, alternates with rest, and continues for a time after the stimulus is withdrawn.

In their mode of responding to these stimuli, all the voluntary muscles, or those with transverse striæ, are alike; but among those with plain or unstriped fibres there are many differences,—a fact which tends to confirm the opinion that their peculiarity depends as well on their connection with nerves and ganglia as on their own properties. According to Weber, the ureters and gall-bladder are the parts least excited by stimuli: they do not act at all till the stimulus has been long applied, and then contract feebly, and to a small extent. The contractions of the cæcum and stomach are quicker and wider-spread: still quicker those of the iris, and of the urinary bladder if it be not too full. The actions of the small and large intestines, of the vas deferens, and pregnant uterus, are yet more vivid, more regular, and more sustained; and they require no more stimulus than that of the air to excite them. The heart, on account, doubtless, of its striated muscle, is the quickest and most vigorous of all the muscles of organic life in contracting upon irritation, and appears in this, as in nearly all other respects, to be the connecting member of the two classes of muscles.

All the muscles retain their property of contracting under the influence of stimuli applied to them or to their nerves for some time after death, the period being longer in cold-blooded than in warm-blooded Vertebrata, and shorter in Birds than in Mammalia. It would seem as if the more active the respiratory

process in the living animal, the shorter is the time of duration of the irritability in the muscles after death; and this is confirmed by the comparison of different species in the same order of Vertebrata. But the period during which this irritability lasts, is not the same in all persons, nor in all the muscles of the same persons. In a man it ceases, according to Nysten, in the following order:—first in the left ventricle, then in the intestines and stomach, the urinary bladder, right ventricle, œsophagus, iris; then in the voluntary muscles of the trunk, lower and upper extremities; lastly in the right and left auricle of the heart.

Rigor.—After the muscles of the dead body have lost their irritability or capability of being excited to contraction by the application of a stimulus, they spontaneously pass into a state of contraction, apparently identical with that which ensues during life. It affects all the muscles of the body; and, where external circumstances do not prevent it, commonly fixes the limbs in that which is their natural posture of equilibrium or rest. Hence, and from the simultaneous contraction of all the muscles of the trunk, is produced a general stiffening of the body, constituting the *rigor mortis* or *post-mortem rigidity.*

When this condition has set in, the muscle becomes acid in reaction (due to lactic acid), and gives off carbonic acid. Its volume is slightly diminished: the muscular fibres become shortened and opaque, and their substance has set firm. It comes on much more rapidly after muscular activity, and is hastened by warmth. It may be brought on, in muscles exposed for experiment, by the action of distilled water and many acids, also by freezing and thawing again.

The immediate cause of rigor seems coagulation of the myosin (Brücke, Kühne, Norris). We may distinguish three main stages.—(1). Gradual coagulation. (2). Contraction of coagulated myosin and squeezing out of muscle-serum. (3). Putrefaction.

After the first stage, restoration is possible through the circulation of arterial blood through the muscles (Brown-Séquard); and even when the second stage has set in, vitality may be

restored by dissolving the coagulum of the muscle in salt solution, and passing arterial blood through its vessels (Hermann, Kühne). In the third stage recovery is impossible.

The muscles are not affected simultaneously by *post-mortem* contraction. It affects the neck and lower jaw first; next, the upper extremities, extending from above downwards; and lastly, reaches the lower limbs; in some rare instances only, it affects the lower extremities before, or simultaneously with, the upper extremities. It usually ceases in the order in which it began; first at the head, then in the upper extremities, and lastly in the lower extremities. It never commences earlier than ten minutes, and never later than seven hours, after death; and its duration is greater in proportion to the lateness of its accession (Sommer). Heat is developed during the passage of a muscular fibre into the condition of rigor mortis (Schiffer).

Since rigidity does not ensue until muscles have lost the capacity of being excited by external stimuli, it follows that all circumstances which cause a speedy exhaustion of muscular irritability, induce an early occurrence of the rigidity, while conditions by which the disappearance of the irritability is delayed, are succeeded by a tardy onset of this rigidity. Hence its speedy occurrence, and equally speedy departure in the bodies of persons exhausted by chronic diseases; and its tardy onset and long continuance after sudden death from acute diseases. In some cases of sudden death from lightning, violent injuries, or paroxysms of passion, rigor mortis has been said not to occur at all; but this is not always the case. It may, indeed, be doubted whether there is really a complete absence of the post-mortem rigidity in any such cases; for the experiments of M. Brown-Séquard with electro-magnetism make it probable that the rigidity may supervene immediately after death, and then pass away with such rapidity as to be scarcely observable.

Brown-Séquard took five rabbits, and killed them by removing their hearts. In the first, rigidity came on in 10 hours, and lasted 192 hours; in the second, which was feebly electrified, it commenced in seven hours, and lasted 144; in the third, which was more strongly electrified, it came on in two, and lasted 72 hours; in the fourth, which was still more strongly electrified, it came on in one hour, and lasted 20; while, in the last rabbit, which was

submitted to a powerful electro-galvanic current, the rigidity ensued in seven minutes after death, and passed away in 25 minutes. From this it appears that the more powerful the electric current, the sooner does the rigidity ensue, and the shorter is its duration; and as the lightning shock is so much more powerful than any ordinary electric discharge, the rigidity may ensue so early after death and pass away so rapidly as to escape detection. The influence exercised upon the onset and duration of post-mortem rigidity by causes which exhaust the irritability of the muscles, was well illustrated in further experiments by the same physiologist, in which he found that the rigor mortis ensued far more rapidly, and lasted for a shorter period in those muscles which had been powerfully electrified just before death than in those which had not been thus acted upon.

The occurrence of rigor mortis is not prevented by the previous existence of paralysis in a part, provided the paralysis has not been attended with very imperfect nutrition of the muscular tissue.

The rigidity affects the involuntary as well as the voluntary muscles, whether they be constructed of striped or unstriped fibres. The rigidity of involuntary muscles with striped fibres is shown in the contraction of the heart after death. The contraction of the muscles with unstriped fibres is shown by an experiment of Valentin, who found that if a graduated tube connected with a portion of intestine taken from a recently-slain animal, be filled with water, and tied at the opposite end, the water will in a few hours rise to a considerable height in the tube, owing to the contraction of the intestinal walls. It is still better shown in the arteries, of which all that have muscular coats contract after death, and thus present the roundness and cord-like feel of the arteries of a limb lately removed, or those of a body recently dead. Subsequently they relax, as do all the other muscles, and feel lax and flabby, and lie as if flattened, and with their walls nearly in contact.*

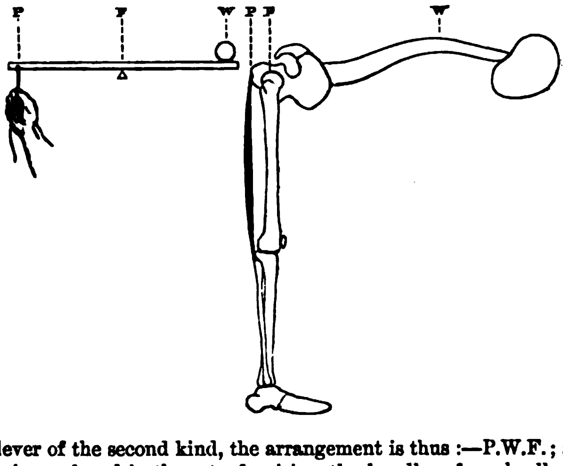
* Although the preceding remarks represent the views generally entertained in regard to muscular action, yet it must be observed that a new and very different theory on the subject has been lately advanced by several writers, and especially developed by Dr. Radcliffe, who has also made it the basis of new views on the pathology of various convulsive affections. According to this doctrine, the ordinary relaxed or elongated state of a muscle is due to a certain "state of polarity" in which the muscle is maintained, and contraction is brought about by anything (such as an effort of the will) which liberates the muscle from this influence, and thus leaves it to the operation

Actions of the Voluntary Muscles.

The greater part of the voluntary muscles of the body act as sources of power for moving levers,—the latter consisting of the various bones to which the muscles are attached.

All levers have been divided into three kinds, according to the relative position of the *power*, the *weight* to be removed, and the *axis of motion* or *fulcrum*. In a lever of the *first* kind the *power* is at one extremity of the lever, the *weight* at the other, and the *fulcrum* between the two. If the initial letters only of the *power*, *weight*, and *fulcrum* be used, the arrangement will stand thus :—P. F.W. A poker, as ordinarily used, or the bar in fig. 272, may be cited as an example of this variety of lever ; while, as an instance in which the bones of the human skeleton are used as a lever of the same kind, may be mentioned the act of raising the body from the stooping posture by means of the hamstring muscles attached to the tuberosity of the ischium (fig. 272).

Fig. 272.

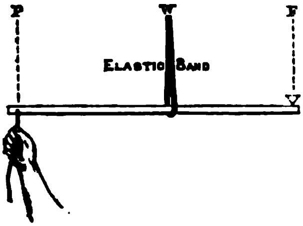


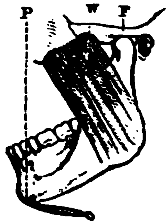
In a lever of the second kind, the arrangement is thus :—P.W.F. ; and this leverage is employed in the act of raising the handles of a wheelbarrow, or in stretching an elastic band as in fig. 273. In the human body the act of opening the mouth by depressing the lower jaw, is an example of the same

of the attractive force inherent in the muscular molecules. According to this doctrine, also, the stage of rigor mortis is readily explicable : death depriving the muscles of the "state of polarity" whereby they had hitherto been kept relaxed, and thus allowing the attractive force of the muscular particles to come into play. For facts and arguments in support of this view, and for references and confirmatory opinions, Dr. Radcliffe's work On Epileptic and other Convulsive Affections may be consulted.

kind,—the tension of the muscles which close the jaw representing the weight (fig. 273).

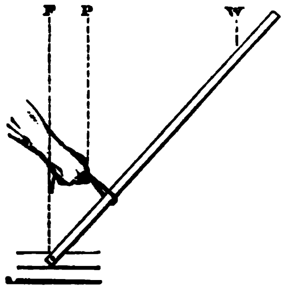
Fig. 273.

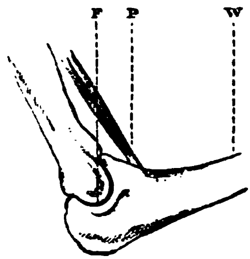




In a lever of the third kind the arrangement is—F.P.W., and the act of raising a pole, as in fig. 274, is an example. In the human body there are numerous examples of the employment of this kind of leverage. The act of bending the fore-arm may be mentioned as an instance (fig. 274). The act of biting is another example.

Fig. 274.





At the ankle we have examples of all three kinds of lever. 1st kind—Extending the foot. 3rd kind—Flexing the foot. In both these cases the foot represents the weight: the ankle joint the fulcrum, the power being the calf muscles in the first case, and the tibialis anticus in the second case. 2nd kind—When the body is raised on tip-toe. Here the ground is the fulcrum, the weight of the body acting at the ankle joint the weight, and the calf muscles the power.

In the human body, levers are most frequently used at a disadvantage as regards power, the latter being sacrificed for the sake of a greater range of motion. Thus in the diagrams of the first and third kinds it is evident that the power is so close to the fulcrum, that great force must be exercised in order to produce motion. It is also evident, however, from the same diagrams, that by the closeness of the power to the fulcrum a great range of movement can be obtained by means of a comparatively slight shortening of the muscular fibres.

The greater number of the more important muscular actions of the human body—those, namely, which are arranged har-

moniously so as to subserve some definite purpose or other in the animal economy—are described in various parts of this work, in the sections which treat of the physiology of the processes by which these muscular actions are resisted or carried out. The combined action of the respiratory muscles, for instance, will be found described in the chapter on "Respiration"; the action of the heart and blood-vessels, under the head of "Circulation"; while the movements of the stomach and intestines are too intimately associated with the function of "Digestion," to be described apart from it. There are, however, one or two very important and somewhat complicated muscular acts which may be best described in this place.

Walking.—In the act of walking, almost every voluntary muscle in the body is brought into play, either directly for purposes of progression, or indirectly for the proper balancing of the head and trunk. The muscles of the arms are least concerned; but even these are for the most part instinctively in action also to some extent.

Among the chief muscles engaged directly in the act of walking are those of the calf, which, by pulling up the heel, pull up also the astragalus, and with it, of course, the whole body, the weight of which is transmitted through the tibia to this bone (fig. 275). When starting to walk, say

Fig. 275.

1 2 3 4 5

with the left leg, this raising of the body is not left entirely to the muscles of the left calf, but the trunk is thrown forward in such a way that it would fall prostrate were it not that the right foot is brought forward and planted on the ground to support it. Thus the muscles of the left calf are assisted in their action by those muscles on the front of the trunk and legs which, by their contraction, pull the body forwards; and of course, if the trunk form a slanting line, with the inclination forwards, it is plain that when the heel is raised by the calf-muscles, the whole body will be raised, and pushed obliquely forwards and upwards. The successive acts in taking the first step in walking are represented in fig. 275, 1, 2, 3.

Now it is evident that by the time the body has assumed the position No. 3, it is time that the right leg should be brought forward to support it

and prevent it from falling prostrate. This advance of the other leg (in this case the *right*) is effected partly by its mechanically swinging forwards, pendulum-wise, and partly by muscular action; the muscles used being,—1*st*, those on the front of the *thigh*, which bend the thigh forwards on the pelvis, especially the rectus femoris, with the psoas and the iliacus; 2*ndly*, the hamstring muscles, which slightly bend the *leg* on the thigh; and 3*rdly*, the muscles on the front of the *leg*, which raise the front of the foot and toes, and so prevent the latter in swinging forwards from hitching in the ground. Anybody who has attentively watched the helpless flapping action of the foot and leg in cases of partial paralysis affecting the muscles of the leg, or who will, in his own case, note the act of bringing the leg forward in walking, will be convinced of the large share which the muscles take in the act in question; although, of course, their work is rendered much easier by the pendulum-like swinging forward of the leg by its own weight.

The second part of the act of walking, which has been just described, is shown in the diagram (4, fig. 275).

When the *right* foot has reached the ground the action of the *left* leg has not ceased. The calf-muscles of the latter continue to act, and by pulling up the heel, throw the body still more forwards over the *right* leg, now bearing nearly the whole weight, until it is time that in *its* turn the *left* leg should swing forwards, and the left foot be planted on the ground to prevent the body from falling prostrate. As at first, while the calf-muscles of one leg and foot are preparing, so to speak, to *push* the body forward and upward from behind by raising the heel, the muscles on the *front* of the trunk and of the same leg (and of the other leg, except when it is swinging forwards) are helping the act by *pulling* the legs and trunk, so as to make them incline forward, the rotation in the inclining forwards being effected mainly at the ankle-joint. Two main kinds of leverage are, therefore, employed in the act of walking, and if this idea be firmly grasped, the detail will be understood with comparative ease. One kind of leverage employed in walking is essentially the same with that employed in pulling forward the pole, as in fig. 274. And the other, less exactly, is that employed in raising the handles of a wheelbarrow. Now, supposing the lower end of the pole to be placed in the barrow, we should have a very rough and inelegant, but not altogether bad representation of the two main levers employed in the act of walking. The body is *pulled* forward by the muscles in front, much in the same way that the pole might be by the force applied at P. (fig. 274) while the raising of the heel and *pushing* forwards of the trunk by the calf-muscles is roughly represented on raising the handles of the barrow. The manner in which these actions are performed alternately by each leg, so that one after the other is swung forwards to support the trunk, which is at the same time *pushed* and *pulled* forwards by the muscles of the other, may be gathered from the previous description.

There is one more thing to be noticed especially in the act of walking. Inasmuch as the body is being constantly supported and balanced on each leg alternately, and therefore on only one at the same moment, it is evident that there must be some provision made for throwing the centre of gravity over the line of support formed by the bones of each leg, as, in its turn, it supports the weight of the body. This may be done in various ways, and the manner in which it is effected is one element in the differences which

exist in the walking of different people. Thus it may be done by an instinctive slight rotation of the pelvis on the head of each femur in turn, in such a manner that the centre of gravity of the body shall fall over the foot of this side. Thus when the body is pushed onwards and upwards by the raising, say, of the *right* heel, as in fig. 275, 3, the pelvis is instinctively, by various muscles, made to rotate on the head of the left femur at the acetabulum, to the left side, so that the weight may fall over the line of support formed by the left leg at the time that the *right* leg is swinging forwards, and leaving all the work of support to fall on its fellow. Such a "rocking" movement of the trunk and pelvis, however, is accompanied by a movement of the whole trunk and leg over the foot which is being planted on the ground (fig. 276); the action being accompanied with a compensatory outward movement at the hip, more easily appreciated by looking at the figure (in which this movement is shown exaggerated) than described.

Fig. 276.

Thus the body in walking is continually rising and swaying alternately from one side to the other, as its centre of gravity has to be brought alternately over one or other leg; and the curvatures of the spine are altered in correspondence with the varying position of the weight which it has to support. The extent to which the body is raised or swayed differs much in different people.

In walking, one foot or the other is always on the ground. The act of *leaping*, or *jumping*, consists in so sudden a raising of the heels by the sharp and strong contraction of the calf-muscles, that the body is jerked off the ground. At the same time the effect is much increased by first bending the thighs on the pelvis, and the legs on the thighs, and then suddenly straightening out the angles thus formed. The share which this action has in producing the effect may be easily known by attempting to leap in the upright posture, with the legs quite straight.

Running is performed by a series of rapid low jumps with each leg alternately; so that, during each complete muscular act concerned, there is a moment when both feet are off the ground.

In all these cases, however, the description of the manner in which any given effect is produced, can give but a very imperfect idea of the infinite number of combined and harmoniously arranged muscular contractions which are necessary for even the simplest acts of locomotion.

Actions of the Involuntary Muscles.—The involuntary muscles

are for the most part not attached to bones arranged to act as levers, but enter into the formation of such hollow parts as require a diminution of their calibre by muscular action, under particular circumstances. Examples of this action are to be found in the intestines, urinary bladder, heart and blood-vessels, gall-bladder, gland-ducts, etc.

The difference in the manner of contraction of the striated and non-striated fibres has been already referred to (p. 598); and the peculiar vermicular or peristaltic action of the latter fibres has been described at p. 368.

Source of Muscular Action.

It was formerly supposed that each act of contraction on the part of a muscle was accompanied by a correlative waste or destruction of its own substance; and that the quantity of the nitrogenous excreta, especially of urea, presumably the expression of this waste, was in exact proportion to the amount of muscular work performed. It has been found, however, both that the theory itself is erroneous, and that the supposed facts on which it was founded do not exist.

It is true that in the action of muscles, as of all other parts, there is a certain destruction of tissue or, in other words, a certain 'wear and tear,' which may be represented by a slight increase in the quantity of urea excreted: but it is not the *correlative* expression or *only* source of the power manifested. The increase in the amount of urea which is excreted after muscular exertion is by no means so great as was formerly supposed; indeed, it is very slight. And as there is no reason to believe that the waste of muscle-substance can be expressed, with unimportant exceptions, in any other way than by an increased excretion of urea, it is evident that we must look elsewhere than in destruction of muscle, for the source of muscular action. For, it need scarcely be said, all force manifested in the living body must be the correlative expression of force previously latent in the food eaten or the tissue formed; and evidences of force expended in the body must be found in the *excreta*. If, therefore, the *nitrogenous* excreta, represented chiefly by urea.

are not in sufficient quantity to account for the work done, we must look to the *non-nitrogenous* excreta as carbonic acid and water, which, presumably, cannot be the expression of wasted muscle-substance.

The quantity of these non-nitrogenous excreta is undoubtedly increased by active muscular efforts, and to a considerable extent; and whatever may be the source of the water, the carbonic acid, at least, is the result of chemical action in the system, and especially of the combustion of non-nitrogenous food, although, doubtless, of nitrogenous food also. We are, therefore, driven to the conclusion,—that the substance of muscles is not wasted in proportion to the work they perform; and that the non-nitrogenous as well as the nitrogenous foods may, in their combustion, afford the requisite conditions for muscular action. The urgent necessity for *nitrogenous* food, especially after exercise, is probably due more to the need of *nutrition* by the exhausted muscles and other tissues for which, of course, nitrogen is essential, than to such food being superior to *non-nitrogenous* substances as a source of muscular power.

Electric Currents in Muscle and Nerve.

If a living muscle or nerve be cut transversely at two points and the intervening portion removed, evidence may be obtained of electric currents passing from the middle of the longitudinal surface to the centre of either of the artificial transverse surfaces made by section. In the case of muscle these currents cease entirely when *rigor mortis* is established.

When a muscle is tetanised by the electric stimulation of its motor nerve, the natural current in the muscle, above described, is diminished or may be even reversed. Similar effects are produced in a nerve by its electric stimulation. This phenomenon has received the name of *Negative Variation*.

An electric current passed through a nerve may increase or diminish the strength of the natural electric current in the nerve. "When a constant electric current enters a nerve, the natural nerve-current even at some distance from the electrodes is affected during the whole time of the passage of the constant

current" (Michael Foster). When these two currents have the same direction, the natural current is increased; when contrary directions, the natural current is diminished. The name *electrotonus* is given to the condition of the nerve which exists during the time of electric stimulation.

If a nerve going to a muscle be irritated by the same electric stimulus successively at two different points, the effect, as evidenced by the force of the muscular contraction, is greater when the stimulus is applied *farther* from the muscle.

The effects of section of a nerve on its electric irritability are as follow:—A temporary increase of irritability follows immediately on section of the nerve, due no doubt to the mechanical irritation of cutting the nerve. This increase is soon, however, succeeded by a diminution of irritability commencing at the point of section and advancing towards the terminal branches where the irritability lingers longest.

Electric currents are conveyed by nerves as well in one direction as another, the differing effects (as to sensation, motion, etc.) in different cases depending on the central and peripheral connections of the nerves, and not on variations in their intimate structure.

If one of the main divisions (peroneal) of the sciatic nerve of a frog be divided and the proximal end be stimulated by an electric current, after division of the sciatic trunk, the muscles supplied by the other main division (tibial) contract. In this case the current must be conducted along the peroneal nerve to the sciatic trunk, and thence downwards along the tibial nerve to the muscles which it supplies; inasmuch as no reflex action through a nerve-centre (spinal cord) is possible on account of the severance of the sciatic trunk. This so-called "paradoxical contraction" of muscle is explained by Du Bois-Reymond on the supposition that the proximity of the fibres belonging to the two branches, in the main trunk, gives an opportunity for the sudden appearance of the electrotonic current in the one to act as a stimulus to the other.

CHAPTER XX.

THE VOICE AND SPEECH.

In nearly all air-breathing vertebrate animals there are arrangements for the production of sound, or *voice*, in some part of the respiratory apparatus. In many animals, the sound admits of being variously modified and altered during and after its production; and, in man, one such modification occurring in obedience to dictates of the cerebrum, is *speech*.

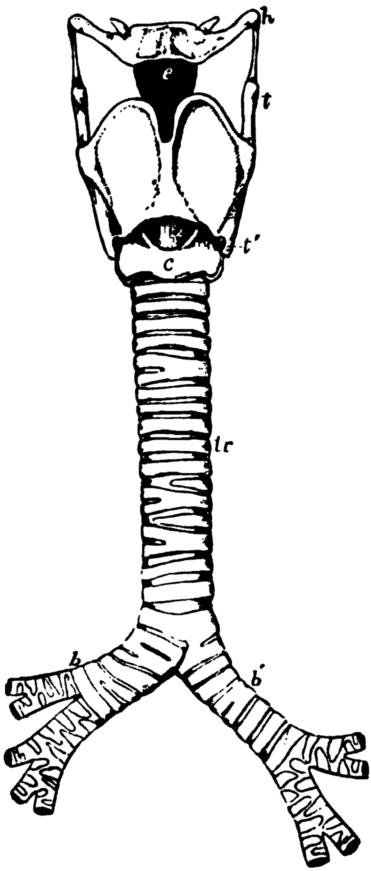
Mode of Production of the Human Voice.

It has been proved by observations on living subjects, by means of the laryngoscope, as well as by experiments on the larynx taken from the dead body, that the sound of the human voice is the result of the inferior laryngeal ligaments, or true vocal cords (A, *cv*, fig. 281) which bound the *glottis*, being thrown into vibration by currents of expired air impelled over their edges. Thus, if a free opening exists in the trachea, the sound of the voice ceases, but returns on the opening being closed. An opening into the air-passages above the glottis, on the contrary, does not prevent the voice being formed. Injury of the laryngeal nerves supplying the muscles which move the vocal cords puts an end to the formation of vocal sounds; and when these nerves are divided on both sides, the loss of voice is complete. Moreover, by forcing a current of air through the larynx in the dead subject, clear vocal sounds are produced, though the epiglottis, the upper ligaments of the larynx or false vocal cords, the ventricles between them and the inferior ligaments or true vocal cords, and the upper part of the arytenoid cartilages, be all removed; provided the true vocal cords remain entire, with their points of attachment, and be kept tense and so approximated that the fissure of the glottis may be narrow.

The vocal ligaments or cord, therefore, may be regarded as the proper organs of the mere voice: the modifications of the voice being effected by other parts—tongue, teeth, lips, etc., as

well as by them. The structure of the vocal cords is adapted to enable them to vibrate like tense membranes, for they are essentially composed of elastic tissue; and they are so attached to the cartilaginous parts of the larynx that their position and tension can be variously altered by the contraction of the muscles which act on these parts.

*Fig. 277.**



The Larynx.

The *larynx*, or organ of voice, consists essentially of the two vocal cords, which are so attached to certain cartilages, and so under the control of certain muscles, that they can be made the means not only of closing the aperture of the larynx (rima glottidis), of which they are the lateral boundaries, against the entrance and exit of air to or from the lungs, but also can be stretched or relaxed, shortened or lengthened, in accordance with the conditions that may be necessary for the air in passing over them, to set them vibrating and produce various sounds. Their action in respiration has been already referred to (p. 236), in

* Fig. 277. Outline showing the general form of the larynx, trachea, and bronchi, as seen from before. ½.—*h*, the great cornu of the hyoid bone; *e*, epiglottis; *t*, superior, and *t′*, inferior cornu of the thyroid cartilage; *c*, middle of the cricoid cartilage; *tr*, the trachea, showing sixteen cartilaginous rings; *b*, the right, and *b′*, the left bronchus. (Allen Thomson).

connection with ordinary tranquil respiration, and also (p. 253, *et seq.*) with other respiratory acts, in which the opening or closing of the glottis, or, in other words, the close apposition or separation of the vocal cords, is an essential part of the performance. In these respiratory acts, however, any sound that may be produced, as in coughing, is, so to speak, an accident, and not performed with purpose. In the present chapter the sound produced by the vibration of the vocal cords is the only part of their function with which we have to deal.

Fig. 278.*

It will be well, perhaps, to refer to a few points in the anatomy of the larynx, before considering its physiology in connection with voice and speech.

The principal parts entering into the formation of the larynx (figs. 277 and 278) are—(*t*) the thyroid cartilage; (*c*) the cricoid cartilage; (*a*) the two arytenoid cartilages; and the two true vocal cords (A, *cc*, fig. 281). The epiglottis (fig. 277 *e*), has but little to do with the voice, and is chiefly useful in falling

* Fig. 278. Outline showing the general form of the larynx, trachea, and bronchi, as seen from behind. ½.—*h*, great cornu of the hyoid bone; *t*, superior, and *t'*, the inferior cornu of the thyroid cartilage: *e*, the epiglottis; *a*, points to the back of both the arytenoid cartilages, which are surmounted by the cornicula; *c*, the middle ridge on the back of the cricoid cartilage; *t r*, the posterior membranous part of the trachea; *b*, *b'*, right and left bronchi. (Allen Thomson).

down as a "lid" over the upper part of the larynx, to help in preventing the entrance of food and drink in deglutiton. It also probably guides mucus or other fluids in small amount from the mouth around the sides of the upper opening of the glottis into the pharynx and œsophagus: thus preventing them from entering the larynx. The false vocal cords (*crs*, fig. 281), and the ventricle of the larynx, which is a space between the false and the true cord of either side, need be here only referred to.

The thyroid cartilage (fig. 279, 1 to 4) does not form a complete ring around the larynx, but only covers the front portion. The cricoid cartilage (fig. 279, 5, 6), on the other hand, is a complete ring; the back part of the ring being much broader than the front. On the top of this broad portion

Fig. 279.*

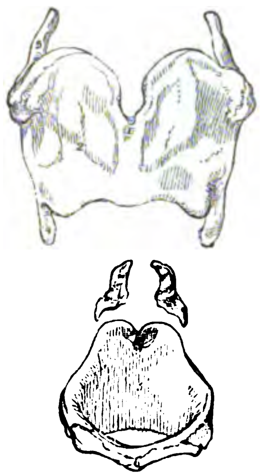
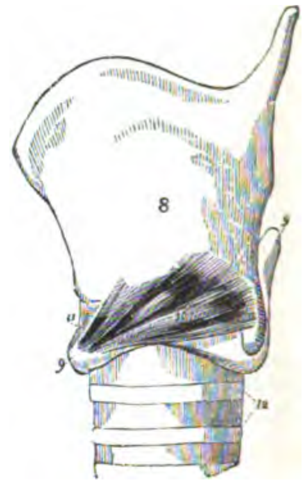


Fig. 280.†



of the cricoid are the arytenoid cartilages (fig. 278, *a*) the connection between the cricoid below and arytenoid cartilages above being a joint with synovial membrane and ligaments, the latter permitting tolerably free motion between them. But, although the arytenoid cartilages can move on the cricoïd, they of course accompany the latter in all their movements, just as the head may nod or turn on the top of the spinal column, but must accompany it in all its movements as a whole.

The thyroid cartilage is also connected with the cricoid, not only by liga-

* Fig. 279. Cartilages of the larynx seen from before. ¾.—1 to 4, thyroid cartilage; 1, vertical ridge or pomum Adami; 2, right ala; 3, superior, and 4, inferior cornu of the right side; 5, 6, cricoid cartilage; 5, inside of the posterior part; 6, anterior narrow part of the ring; 7, arytenoid cartilages.

† Fig. 280. Lateral view of exterior of the larynx; 8, Thyroid cartilage; 9, Cricoid cartilage; 10, Crico-thyroid muscle; 11, Crico-thyroid ligament; 12, first rings of trachea (Willis).

ments, but by two joints with synovial membrane (t′, figs. 277 and 278); the lower *cornua* of the thyroid clasping, or nipping, as it were, the cricoid between them, but not so tightly but that the thyroid can revolve, within a certain range, around an axis passing transversely through the two joints at which the cricoid is clasped. The vocal cords are attached (behind) to the front portion of the base of the arytenoid cartilages, and (in front) to the re-entering angle at the back part of the thyroid; it is evident, therefore, that all movements of either of these cartilages must produce an effect on them of some kind or other. Inasmuch, too, as the arytenoid cartilages rest on the top of the back portion of the cricoid cartilage (*a*, fig. 278), and are connected with it by capsular and other ligaments, all movements of the cricoid cartilage must move the arytenoid cartilages, and also produce an effect on the vocal cords.

The so-called *intrinsic* muscles of the larynx, or those which, in their action, have a direct action on the vocal cords, are nine in number—four pairs, and a single muscle; namely, two *crico-thyroid* muscles, two *thyro-arytenoid*, two *posterior crico-arytenoid*, two *lateral crico-arytenoid*, and one *arytenoid* muscle. Their actions are as follow:—When the *crico-thyroid* muscles (10, fig. 280) contract, they rotate the cricoid on the thyroid cartilage in such a manner that the upper and back part of the former, and of necessity the arytenoid cartilages on the top of it, are tipped backwards, while the thyroid is inclined forward: and thus, of course, the vocal cords being attached in front to one, and behind to the other, are "put on the stretch."

The *thyro-arytenoid* muscles (7, fig. 283), on the other hand, have an opposite action,—pulling the *thyroid* backwards, and the *arytenoid* and upper and back part of the *cricoid* cartilages forwards, and thus *relaxing* the vocal cords.

The *crico-arytenoidei postici* muscles (fig. 282, *b*) *dilate* the glottis, and separate the vocal cords, the one from the other, by an action on the arytenoid cartilage, which will be plain on reference to B′ and C′, (fig. 281). By their contraction they tend to *pull together* the outer angles of the arytenoid cartilages in such a fashion as to rotate the latter at their joint with the cricoid, and of course to throw asunder their anterior angles to which the vocal cords are attached.

These *posterior* crico-arytenoid muscles are opposed by the *crico-arytenoidei laterales*, which, pulling in the opposite direction from the other side of the axis of rotation, have of course exactly the opposite effect, and close the glottis (fig. 283, 4 and 5).

The aperture of the glottis can be also contracted by the *arytenoid* muscle (*s*, fig. 282, and 6, fig. 283), which, in its contraction, pulls together the upper parts of the arytenoid cartilages between which it extends.

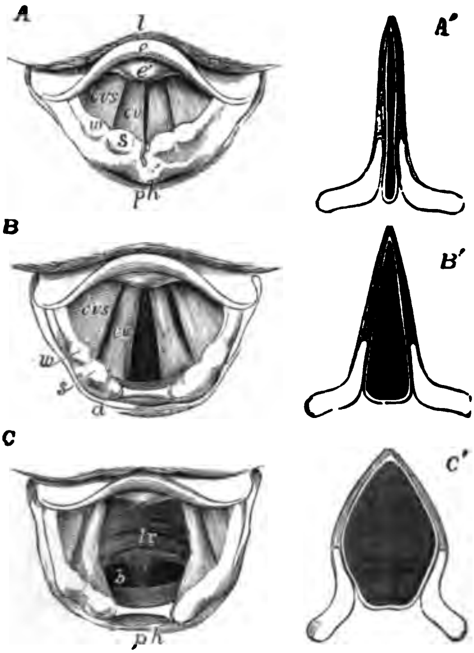
In the performance of the functions of the larynx, the sensory filaments of the pneumogastric supply that acute sensibility by which the glottis is guarded against the ingress of foreign bodies, or of irrespirable gases. The contact of these stimulates the filaments of the superior laryngeal branch of the pneumogastric; and the impression conveyed to the medulla oblongata, whether it produce sensation or not, is reflected to the filaments of the recurrent or inferior laryngeal branch, and excites contraction of the muscles that close the glottis. Both these branches of the pneumogastric co-operate

also in the production and regulation of the voice; the inferior laryngeal determining the contraction of the muscles that vary the tension of the vocal cords, and the superior laryngeal conveying to the mind the sensations of the state of these muscles necessary for their continuous guidance. And both the branches co-operate in the actions of the larynx in the ordinary slight dilatation and contraction of the glottis in the acts of expiration and inspiration, and more evidently in those of coughing and other forcible respiratory movements.

The placing of the vocal cords in a position parallel one with the other, is effected by a combined action of the various little muscles which act on them—the thyro-arytenoidei having, without much reason, the credit of taking the largest share in the production of this effect. Fig. 281 is intended to show the various positions of the vocal cords under different circumstances. Thus, in ordinary tranquil breathing, the opening of the glottis is wide and triangular (B) becoming a little wider at each inspiration, and a little narrower at each expiration. On making a rapid and deep inspiration the opening of the glottis is widely dilated (as in C), and somewhat lozenge-shaped. At the moment of the emission of sound, it is narrowed, the margins of the arytenoid cartilages being brought into contact, and the edges of the vocal cords approximated and made parallel, at the same time that their tension is much increased. The higher the note produced, the tenser do the cords become (fig. 281, A); and the range of a voice depends, of course, in the main, on the extent to which the degree of tension of the vocal cords can be thus altered. In the production of a high note, the vocal cords are brought well within sight, so as to be plainly visible with the help of the laryngoscope. In the utterance of grave tones, on the other hand, the epiglottis is depressed and brought over them, and the arytenoid cartilages look as if they were trying to hide themselves under it (fig. 284).

The *epiglottis*, by being somewhat pressed down so as to cover the superior cavity of the larynx, serves to render the notes deeper in tone, and at the same time somewhat duller, just as covering the end of a short tube placed in front of caoutchouc tongues lowers the tone. In no other respect does the epiglottis appear to have any effect in modifying the vocal sounds.

Fig. 281.*



* Fig. 281. Three laryngoscopic views of the superior aperture of the larynx and surrounding parts and different states of the glottis during life (Czermak).

A, the glottis during the emission of a high note in singing; B, in easy and quiet inhalation of air; C, in the state of widest possible dilatation, as in inhaling a very deep breath. The diagrams A′, B′, and C′, have been added to Czermak's figures, to show in horizontal sections of the glottis the position of the vocal ligaments and arytenoid cartilages in the three several states represented in the other figures. In all the figures, so far as marked, the letters indicate the parts as follow, viz.: *l*, the base of the tongue; *e*, the upper free part of the epiglottis; *é*, the tubercle or cushion of the epiglottis; *ph*, part of the anterior wall of the pharynx behind the larynx; in the margin of the aryteno-epiglottidean fold *w*, the swelling of the membrane caused by the cartilages of Wrisberg; *s*, that of the cartilages of Santorini; *a*, the tip or summit of the arytenoid cartilages; *c v*, the true vocal cords or lips of the rima glottidis; *c v s*, the superior or false vocal cords; between them the ventricle of the larynx; in C, *tr* is placed on the anterior wall of the receding trachea, and *b* indicates the commencement of the two bronchi beyond the bifurcation which may be brought into view in this state of extreme dilatation (from Quain's Anatomy).

The degree of approximation of the vocal cords also usually corresponds with the height of the note produced; but probably

Fig. 282.*

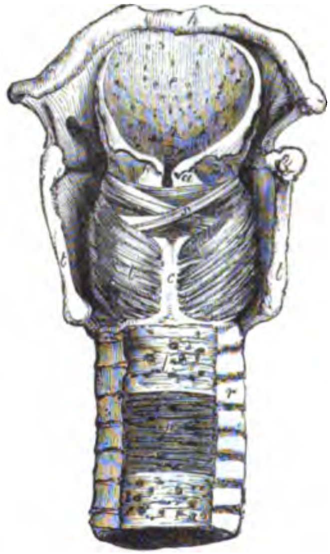
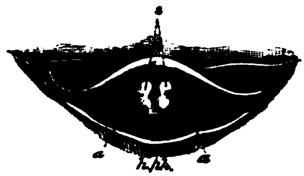


Fig. 283.†

Fig. 284.‡



not always, for the width of the aperture has no essential

* Fig. 282. View of the larynx and part of the trachea from behind, with the muscles dissected; *h*, the body of the hyoid bone; *e*, epiglottis; *t*, the posterior borders of the thyroid cartilage; *c*, the median ridge of the cricoid: *a*, upper part of the arytenoid; *s*, placed on one of the oblique fasciculi of the arytenoid muscle; *b*, left posterior crico-arytenoid muscle; ends of the incomplete cartilaginous rings of the trachea; *l*, fibrous membrane crossing the back of the trachea; *n*, muscular fibres exposed in a part (from Quain's Anatomy).

† Fig. 283. View of the interior of larynx from above. 1, aperture of glottis; 2, arytenoid cartilages; 3, vocal cords; 4, posterior crico-arytenoid muscles; 5, lateral crico-arytenoid muscle of right side, that of left side removed; 6, arytenoid muscle; 7, thyro-arytenoid muscle of left side, that of right side removed; 8, thyroid cartilage; 9, cricoid cartilage; 13, posterior crico-arytenoid ligament. With the exception of the arytenoid muscle, this diagram is a copy from Mr. Willis's figure.

‡ Fig. 284. View of the upper part of the larynx as seen by means of the laryngoscope during the utterance of a grave note. *e*, epiglottis; *s*, tubercles of the cartilages of Santorini; *a*, arytenoid cartilages; *z*, base of the tongue; *ph*, the posterior wall of the pharynx (Czermak).

influence on the height of the note, as long as the vocal cords have the same tension; only with a wide aperture, the tone is more difficult to produce, and is less perfect, the rushing of the air through the aperture being heard at the same time.

No true vocal sound is produced at the posterior part of the aperture of the glottis, that, viz., which is formed by the space between the arytenoid cartilages. For, as Müller's experiments showed, if the arytenoid cartilages be approximated in such a manner that their anterior processes touch each other, but yet leave an opening behind them as well as in front, no second vocal tone is produced by the passage of the air through the posterior opening, but merely a rustling or bubbling sound; and the height or pitch of the note produced is the same whether the posterior part of the glottis be open or not, provided the vocal cords maintain the same degree of tension.

Application of the Voice in Singing and Speaking.

The notes of the voice thus produced may observe three different kinds of sequence. The first is the monotonous, in which the notes have nearly all the same pitch as in ordinary speaking; the variety of the sounds of speech being due to articulation in the mouth. In speaking, however, occasional syllables generally receive a higher intonation for the sake of accent. The second mode of sequence is the successive transition from high to low notes, and *vice versâ,* without intervals; such as is heard in the sounds, which, as expressions of passion, accompany crying in men, and in the howling and whining of dogs. The third mode of sequence of the vocal sounds is the musical, in which each sound has a determinate number of vibrations, and the numbers of the vibrations in the successive sounds have the same relative proportions that characterise the notes of the musical scale.

The *compass of the voice* in different individuals comprehends one, two, or three octaves. In singers—that is, in persons apt for singing—it extends to two or three octaves. But the male and female voices commence and end at different points of the musical scale. The lowest note of the female voice is about an

octave higher than the lowest of the male voice; the highest note of the female voice about an octave higher than the highest of the male. The compass of the male and female voices taken together, or the entire scale of the human voice, includes about four octaves. The principal difference between the male and female voice is, therefore, in their *pitch*; but they are also distinguished by their *tone*,—the male voice is not so soft.

The voice presents other varieties besides that of male and female; there are two kinds of male voice, technically called the bass and tenor, and two kinds of female voice, the contralto and soprano, all differing from each other in tone. The bass voice usually reaches lower than the tenor and its strength lies in the low notes; while the tenor voice extends higher than the bass. The contralto voice has generally lower notes than the soprano, and is strongest in the lower notes of the female voice; while the soprano voice reaches higher in the scale. But the difference of compass, and of power in different parts of the scale, is not the essential distinction between the different voices; for bass singers can sometimes go very high, and the contralto frequently sings the high notes like soprano singers. The essential difference between the bass and tenor voices, and between the contralto and soprano, consist in their tone or 'timbre,' which distinguishes them even when they are singing the same note. The qualities of the barytone and mezzo-soprano voices are less marked; the barytone being intermediate between the bass and tenor, the mezzo-soprano between the contralto and soprano. They have also a middle position as to pitch in the scale of the male and female voices.

The different pitch of the male and the female voices depends on the different length of the vocal cords in the two sexes; their relative length in men and women being as three to two. The difference of the two voices in tone or 'timbre,' is owing to the different nature and form of the resounding walls, which in the male larynx are much more extensive, and form a more acute angle anteriorly. The different qualities of the tenor and bass, and of the alto and soprano voices, probably depend on some peculiarities of the ligaments, and the membranous and cartilaginous parietes of the laryngeal cavity, which are not at present understood, but of which we may form some idea, by recollecting that musical instruments made of different materials, *e.g.*, metallic and gut-strings, may be tuned to the same note, but that each will give it with a peculiar tone or 'timbre.'

The larynx of boys resembles the female larynx; their vocal cords before puberty have not two-thirds the length which they acquire at that period; and the angle of their thyroid cartilage is as little prominent as in the female larynx. Boys' voices are alto and soprano, resembling in pitch those of women, but louder, and differing somewhat from them in tone. But, after the larynx has undergone the change produced during the

period of development at puberty, the boy's voice becomes bass or tenor. While the change of form is taking place, the voice is said to 'crack;' it becomes imperfect, frequently hoarse and crowing, and is unfitted for singing until the new tones are brought under command by practice. In eunuchs, who have been deprived of the testes before puberty, the voice does not undergo this change. The voice of most old people is deficient in tone, unsteady, and more restricted in extent: the first defect is owing to the ossification of the cartilages of the larynx and the altered condition of the vocal cord; the want of steadiness arises from the loss of nervous power and command over the muscles; the result of which is here, as in other parts, a tremulous motion. These two causes combined render the voices of old people void of tone, unsteady, bleating, and weak.

In any class of persons arranged, as in an orchestra, according to the characters of voices, each would possess, with the general characteristics of a bass, or tenor, or any other kind of voice, some peculiar character by which his voice would be recognised from all the rest. The conditions that determine these distinctions are, however, quite unknown. They are probably inherent in the tissues of the larynx, and are as indiscernible as the minute differences that characterize men's features; one often observes, in like manner, hereditary and family peculiarities of voice, as well marked as those of the limbs or face.

Most persons, particularly men, have the power, if at all capable of singing, of modulating their voices through a double series of notes of different character: namely, the notes of the natural voice, or *chest-notes*, and the *falsètto notes*. The natural voice, which alone has been hitherto considered, is fuller, and excites a distinct sensation of much stronger vibration and resonance than the falsetto voice, which has more a flute-like character. The deeper notes of the male voice can be produced only with the natural voice, the highest with the falsetto only; the notes of middle pitch can be produced either with the natural or falsetto voice; the two registers of the voice are therefore not limited in such a manner as that one ends when the other begins, but they run in part side by side.

The natural or chest-notes, are produced by the ordinary vibrations of the vocal cords. The mode of production of the falsetto notes is still obscure.

By Müller the falsetto notes were thought to be due to vibrations of only the inner borders of the vocal cords. In the opinion of Petrequin and Diday, they do not result from vibrations of the vocal cords at all, but from vibrations of the air passing through the aperture of the glottis, which they believe assumes, at such times, the contour of the *embouchure* of a flute. Others (considering some degree of similarity which exists between the falsetto notes, and the peculiar tones called harmonic, which are produced when, by touching or stopping a harp-string at a particular point, only a portion of its length is allowed to vibrate) have supposed that, in the falsetto notes, portions of the vocal ligaments are thus isolated, and made to vibrate while the rest are held still. The question cannot yet be settled; but any one in the habit of singing may assure himself, both by the difficulty of passing smoothly from one set of notes to the other, and by the necessity of exercising himself in both registers, lest he should become very deficient in one, that there must be some great difference in the modes in which their respective notes are produced.

The strength of the voice depends partly on the degree to which the vocal cords can be made to vibrate; and partly on the fitness for resonance of the membranes and cartilages of the larynx, of the parietes of the thorax, lungs, and cavities of the mouth, nostrils, and communicating sinuses. It is diminished by anything which interferes with such capability of vibration. The intensity or loudness of a given note with maintenance of the same 'pitch,' cannot be rendered greater by merely increasing the force of the current of air through the glottis; for increase of the force of the current of air, *cæteris paribus*, raises the pitch both of the natural and the falsetto notes. Yet, since a singer possesses the power of increasing the loudness of a note from the faintest 'piano' to 'fortissimo' without its pitch being altered, there must be some means of compensating the tendency of the vocal cords to emit a higher note when the force of the current of air is increased. This means evidently consists in modifying the tension of the vocal cords. When a note is rendered louder and more intense, the vocal cords must be relaxed by remission of the muscular action, in proportion as the force of the current of the breath through the glottis is increased. When a note is rendered fainter, the reverse of this must occur.

The *arches of the palate and the uvula* become contracted during the formation of the higher notes; but their contraction is the same for a note of given height, whether it be falsetto or not; and in either case the arches of the palate may be touched with the finger, without the note being altered. Their action, therefore, in the production of the higher notes seems to be merely the result of involuntary associate nervous action, excited by the voluntarily increased exertion of the muscles of the larynx. If the palatine arches contribute at all to the production of the higher notes of the natural voice and the falsetto, it can only be by their increased tension strengthening the resonance.

The office of the *ventricles of the larynx* is evidently to afford a free space for the vibrations of the lips of the glottis; they may be compared with the cavity at the commencement of the mouth-piece of trumpets, which allows the free vibration of the lips.

SPEECH.

Besides the musical tones formed in the larynx, a great number of other sounds can be produced in the vocal tubes, between the glottis and the external apertures of the air-passages, the combination of which sounds by the agency of the cerebrum into different groups to designate objects, properties, actions, etc., constitutes *language*. The languages do not employ all the sounds which can be produced in this manner, the combination of some with others being often difficult. Those sounds which are easy of combination enter, for the most part, into the formation of the greater number of languages. Each language contains a certain number of such sounds, but in no one are all brought together. On the contrary, different languages are characterised by the prevalence in them of certain classes of these sounds, while others are less frequent or altogether absent.

The sounds produced in speech, or *articulate sounds*, are commonly divided into *vowels* and *consonants*; the distinction between which is, that the sounds for the former are generated by the larynx, while those for the latter are produced by

interruption of the current of air in some part of the air-passages above the larynx. The term consonant has been given to these because several of them are not properly sounded, except *consonantly with* a vowel. Thus, if it be attempted to pronounce aloud the consonants *b*, *d*, and *g*, or their modifications, *p*, *t*, *k*, the intonation only follows them in their combination with a vowel.

To recognize the essential properties of the articulate sounds, we must, according to Müller, first examine them as they are produced in whispering, and then investigate which of them can also be uttered in a modified character conjoined with vocal tone. By this procedure we find two series of sounds: in one the sounds are mute, and cannot be uttered with a vocal tone; the sounds of the other series can be formed independently of voice, but are also capable of being uttered in conjunction with it.

All the vowels can be expressed in a whisper without vocal tone, that is, mutely. These mute vowel-sounds differ, however, in some measure, as to their mode of production, from the consonants. All the mute consonants are formed in the vocal-tube above the glottis, or in the cavity of the mouth or nose, by the mere rushing of the air between the surfaces differently modified in disposition. But the sound of the vowels, even when mute, has its source in the glottis, though its vocal cords are not thrown into the vibrations necessary for the production of voice; and the sound seems to be produced by the passage of the current of air between the relaxed vocal cords. The same vowel sound can be produced in the larynx when the mouth is closed, the nostrils being open, and the utterance of all vocal tone avoided. This sound, when the mouth is open, is so modified by varied forms of the oral cavity, as to assume the characters of the vowels *a*, *e*, *i*, *o*, *u*, in all their modifications.

The cavity of the mouth assumes the same form for the articulation of each of the mute vowels as for the corresponding vowel when vocalized; the only difference in the two cases lies in the kind of sound emitted by the larynx. Krantzenstein and Kempelen have pointed out that the conditions necessary for changing one and the same sound into the different vowels, are

differences in the size of two parts—the oral canal and the oral opening; and the same is the case with regard to the mute vowels. By oral canal, Kempelen means here the space between the tongue and palate: for the pronunciation of certain vowels both the opening of the mouth and the space just mentioned are widened; for the pronunciation of other vowels both are contracted; and for others one is wide, the other contracted. Admitting five degrees of size, both of the opening of the mouth and of the space between the tongue and palate, Kempelen thus states the dimensions of these parts for the following vowel sounds:—

Vowel.	Sound.	Size of oral opening.	Size of oral canal.
a	as in 'far'	5	3
a	„ 'name'	4	2
e	„ 'theme'	3	1
o	„ 'go'	2	4
oo	„ 'cool'	1	5

Another important distinction in articulate sounds is, that the utterance of some is only of momentary duration, taking place during a sudden change in the conformation of the mouth, and being incapable of prolongation by a continued expiration. To this class belong *b*, *p*, *d*, and the hard *g*. In the utterance of other consonants the sounds may be *continuous*; they may be prolonged, *ad libitum*, as long as a particular disposition of the mouth and a constant expiration are maintained. Among these consonants are *h*, *m*, *n*, *f*, *s*, *r*, *l*. Corresponding differences in respect to the time that may be occupied in their utterance exist in the vowel-sounds, and principally constitute the differences of long and short syllables. Thus, the *a* as in "far" and "fate," the *o* as in "go" and "fort," may be indefinitely prolonged; but the same vowels (or more properly different vowels expressed by the same letters), as in "can" and "fact," in "dog" and "rotten," cannot be prolonged.

All sounds of the first or explosive kind are insusceptible of combination with vocal tone ("intonation"), and are absolutely mute; nearly all the consonants of the second or continuous kind may be attended with "intonation."

The peculiarity of speaking, to which the term *ventriloquism*

is applied, appears to consist merely in the varied modification of the sounds produced in the larynx, in imitation of the modifications which voice ordinarily suffers from distance, etc. From the observations of Müller and Colombat, it seems that the essential mechanical parts of the process of ventriloquism consist in taking a full inspiration, then keeping the muscles of the chest and neck fixed, and speaking with the mouth almost closed, and the lips and lower jaw as motionless as possible, while air is very slowly expired through a very narrow glottis; care being taken also, that none of the expired air passes through the nose. But, as observed by Müller, much of the ventriloquist's skill in imitating the voices coming from particular directions, consists in deceiving other senses than hearing. We never distinguish very readily the direction in which sounds reach our ear; and, when our attention is directed to a particular point, our imagination is very apt to refer to that point whatever sounds we may hear.

The tongue, which is usually credited with the power of speech,—*language* and speech being often employed as synonymous terms—plays only a subordinate, although very important part. This is well shown by cases in which nearly the whole organ has been removed on account of disease. Patients who recover from this operation talk imperfectly, and their voice is considerably modified; but the loss of speech is confined to those letters, in the pronunciation of which the tongue is concerned.

Stammering depends on a want of harmony between the action of the muscles (chiefly abdominal) which expel air through the larynx, and that of the muscles which guard the orifice (rima glottidis) by which it escapes, and of those (of tongue, palate, etc.) which modulate the sound to the form of speech.

Over either of the groups of muscles, by itself, a stammerer may have as much power as other people. But he cannot harmoniously arrange their conjoint actions.

This discord of muscles, Sir J. Paget observes, occurs in other organs than those of speech, and most evidently in those of deglutition, micturition, and defæcation.

In the case of "stammering urinary organs," he remarks, "the patient can often pass his urine without any trouble, especially at customary times and places, and when he does so, the stream is full and strong, and he has nothing the matter with him. But at other times he suffers all the distress that he might have with a very bad urethral stricture. He cannot pass a drop of urine; or, after a few drops, there comes a painful check, and the more he strains the less he passes, and then complete retention may ensue, and overfilling of the bladder. . . . . The stammering with the bladder occurs in just the same conditions as the stammering speech. There are few stammerers in speech so bad but that they can talk or read fluently when they are alone or with those whom they are most familiar with, or when they are entirely thoughtless as to their manner of speaking. Their worst times are when with strangers, or with persons or in places that are associated in their minds with stammering. It is just so with the bladder and urethra. . . . . Nearly all the phenomena of stammering speech find in them their parallel. In both alike are observed the strong influence of habit and association of ideas; the effects of transient changes in the vigour of the nervous system; the need of a justly and almost unconsciously measured exercise of the will, that it should be neither more nor less than enough; and the influence of distraction of mind."

CHAPTER XXI.

THE SENSES.

THROUGH the medium of the Nervous system the mind obtains a knowledge of the existence both of the various parts of the body, and of the external world.

This knowledge is based upon *sensations* resulting from the stimulation of certain centres in the brain, by irritations conveyed to them by afferent (sensory) nerves. Under normal circumstances, the following structures are necessary for sensation: (*a*) A peripheral organ for the reception of the impression; (*b*) a nerve for conducting it; (*c*) a nerve-centre for feeling or perceiving it.

Sensations may be conveniently classed as *common* and *special*.

Common Sensations.

Under this head fall all those general sensations which cannot be distinctly localized in any particular part of the body, such as Fatigue, Discomfort, Faintness, Satiety, together with Hunger and Thirst, in which, in addition to a general discomfort, there

is in many persons a distinct sensation referred to the stomach or fauces. In this class must also be placed the various irritations of the mucous membrane of the bronchi, which give rise to coughing, and also the sensations derived from various viscera indicating the necessity of expelling their contents; *e.g.*, the desire to defæcate, to urinate, and, in the female, the sensations which precede the expulsion of the fœtus. We must also include such sensations as itching, creeping, tickling, tingling, burning, aching, etc., some of which come under the head of *pain:* they will be again referred to in describing the sense of *Touch.*

It is impossible to draw a very clear line of demarcation between many of the common sensations above mentioned, and the sense of Touch, which forms the connecting link between the general and special sensations. Touch is, indeed, usually classed with the special senses, and will be considered in the same group with them: yet it differs from them in being common to many nerves; *e.g.*, all the sensory spinal nerves, the pneumogastric, glosso-pharyngeal, and fifth cerebral nerves, and in its impressions being communicable through many organs.

Among common sensations must also be ranked the so-called "muscular sense," which has been already alluded to (p. 535). It is by means of this sense that we become aware of the condition of contraction or relaxation of the various muscles and groups of muscles, and thus obtain the information necessary for their adjustment to various purposes—standing, walking, grasping, etc. This muscular sensibility is shown in our power to estimate the differences between weights by the different muscular efforts necessary to raise them. Considerable delicacy may be attained by practice, and the difference between 19½ oz. in one hand and 20 oz. in the other is readily appreciated (Weber).

This sensibility with which the muscles are endowed must be carefully distinguished from the sense of *contact* and of *pressure*, of which the skin is the organ. When standing erect, we can feel the ground (contact), and further there is a sense of *pressure*, due to our feet being pressed against the ground by the weight of the body. Both these are derived from the skin

of the sole of the foot. If now we raise the body on the toes, we are conscious (muscular sense) of a muscular effort made by the muscles of the calf, which overcomes a certain resistance.

The distinctness of the muscular sense is well illustrated in the following case mentioned by Brown-Séquard.

"Muscular sensibility alone is sufficient for the direction of voluntary movements. I have seen a child completely deprived of cutaneous sensibility (unable to feel contact, pressure, pricking, pinching, tickling, cold or heat), yet able to walk well without looking at its feet, and undoubtedly owing this power to the persistence of guiding sensations in the muscles. In this case, besides the peculiar sensibility which guides voluntary movements, the muscles had the power of giving pain. When they were excited to contract spasmodically, the patient had the feeling of cramps."

Special Sensations.

Including the sense of touch, the special senses are five in number—Touch, Taste, Smell, Hearing, Sight.

The two last are distinguished from the rest in possessing a very complex sense-organ.

Smell, like Sight and Hearing, has but a single nerve appropriated to it, while the sense of Taste appears to be common to branches (gustatory) of the fifth and of the glosso-pharyngeal nerves. These two senses, together with that of Touch, although perfectly distinct, yet often co-operate to produce a complex sensation in which it is difficult to assign to each sense its precise share. Thus, when food is taken into the mouth it is almost impossible to say what part of the sensation produced is due to Touch, Taste, and Smell respectively.

The most important distinction between common and special sensations is that by the former we are made aware of certain conditions of various parts of our bodies, while from the latter we gain our knowledge of the external world also. This difference will be clear if we compare the sensations of pain and touch, the former of which is a common, the latter a special sensation. "If we place the edge of a sharp knife on the skin, we feel the edge by means of our sense of touch; we perceive a sensation, and refer it to the object which has caused it. But as soon as we cut the skin with the knife, we feel pain, a feeling

which we no longer refer to the cutting knife, but which we feel within ourselves, and which communicates to us the fact of a change of condition in our own body. By the sensation of pain we are neither able to recognise the object which caused it, nor its nature" (Weber). Before describing the special senses in detail it will be necessary to point out a few of their general characteristics.

In studying the phenomena of sensation, it is important clearly to understand that the *Sensorium*, or seat of sensation, is in the Brain, and not in the particular organ (eye, ear, etc.) through which the sensory impression is received. In common parlance we are said to *see* with the eye, *hear* with the ear, etc., but in reality these organs are only adapted to receive impressions which are conducted to the sensorium, through the optic and auditory nerves respectively, and there give rise to sensation.

Hence, if the optic nerve is severed (although the eye itself is perfectly uninjured), vision is no longer possible; since, although the image falls on the retina as before, the sensory impression can no longer be conveyed to the sensorium.

When any given sensation is felt, all that we can with certainty affirm is that the sensorium in the brain is excited. The exciting cause may be (in the vast majority of cases is), some object of the external world (*objective sensation*); or the condition of the sensorium may be due to some excitement within the brain, in which case the sensation is termed *subjective*. The mind habitually refers sensations to external causes; and hence, whenever they are subjective (due to causes within the brain), we can hardly divest ourselves of the idea of an external cause, and an *illusion* is the result.

Numberless examples of such illusions might be quoted. As familiar cases may be mentioned, humming and buzzing in the ears caused by some irritation of the auditory nerve or centre, and even musical sounds and voices (sometimes termed auditory spectra); also so-called optical illusions: persons and other objects are described as being seen, although not present.

Such illusions are most strikingly exemplified in cases of delirium tremens or other forms of delirium, in which cats, rats, creeping loathsome forms, etc, are described by the patient as seen with great vividness.

One uniform *internal* cause, which may act on all the nerves

of the senses in the same manner, is the accumulation of blood in their capillary vessels, as in congestion and inflammation. This one cause excites in the retina, while the eyes are closed, the sensations of light and luminous flashes; in the auditory nerve, the sensation of humming and ringing sounds; in the olfactory nerve, the sense of odours; and in the nerves of feeling, the sensation of pain. In the same way, also, a narcotic substance introduced into the blood, excites in the nerves of each sense peculiar symptoms: in the optic nerves, the appearance of luminous sparks before the eyes; in the auditory nerves, "tinnitus aurium"; and in the common sensory nerves, the sensation of creeping over the surface. So, also, among *external* causes, the stimulus of electricity, or the mechanical influence of a blow, concussion, or pressure, excites in the eye the sensation of light and colours; in the ear, a sense of a loud sound or of ringing; in the tongue, a saline or acid taste; and in the other parts of the body, a perception of peculiar jarring or of the mechanical impression, or a shock like it.

The habit of constantly referring our sensations to external causes, lead us to interpret the various modifications which external objects produce in our sensations, as *properties* of the external bodies themselves. Thus we speak of certain substances as possessing a disagreeable taste and smell; whereas, the fact is, their taste and smell are only disagreeable to *us*: for what is loathsome and disgusting to us (such as carrion), is devoured with avidity by vultures, and must, therefore, be agreeable to them. It is evident, however, that on this habit of referring our sensations to causes outside ourselves, depends the reality of the external world to us; and more especially is this the case with the senses of touch and sight. By the co-operation of these two senses aided by the others, we are enabled gradually to attain a knowledge of external objects which daily experience confirms, until we come to place unbounded confidence in what is termed the "evidence of the senses."

The various illusions to which we are thus liable, will be discussed more at length in describing each individual sense: it is sufficient here to point out the distinction which we must draw

between mere sensations, and the judgments based, often unconsciously, upon them.

Thus, in looking at a near object, we unconsciously estimate its distance, and say it seems to be ten or twelve feet off: but the estimate of its distance is in reality a *judgment* based on many things besides the appearance of the object itself; among which may be mentioned the number of intervening objects, the number of steps which from past experience we know we must take before we could touch it, and many others.

The curious illusions which occur in cases of amputation may be also cited as examples.

After the amputation of a leg for instance, sensations are felt for weeks, which are referred to the lost leg or foot, and so entire and persistent is the illusion, that patients not unfrequently attempt to put the foot down to the ground, entirely forgetting that the leg has been amputated. In such cases there is no erroneous *sensation*, but an erroneous *judgment*, which refers the various sensations resulting from irritation of the severed nerve, to its peripheral terminations, on which impressions were usually made (p. 493).

The importance of the special senses is at once obvious when we remember that the *whole* of the knowledge possessed by anyone has been acquired through the medium of his five senses: and the extent to which our conceptions are dependent upon the experience derived through our senses is curiously illustrated by the fact that it is nearly impossible to conceive of a sixth sense as distinct from any of the five as they are from each other. The sensations derived from our sense-organs, are entirely distinct from each other; and though, under normal conditions, each requires for its production the action of a specific exciting cause *e g.*, light in the case of the eye, sound in the case of the ear, yet every stimulation (mechanical, electrical, &c.,) of a nerve of special sense gives rise to its own special sensation, and *not* to pain as in the case of ordinary sensory nerves. Thus, irritation of the optic nerve, as by cutting it, invariably produces a sensation of light, of the auditory nerve a sensation of some modification of sound.

Doubtless these distinct sensations depend not on any speciality in the structure of the nerves of special sense, but on the nature of their connections in the sensorium.

It has been supposed, indeed, that irritation of a nerve of special sense, when excessive, may produce pain; but experiments seem to have proved that none of these nerves possess the faculty of common sensibility. Thus, Magendie observed that when the olfactory nerves, laid bare in a dog, were pricked, no signs of pain were manifested; and other experiments of his seem to show that both the retina and optic nerve are insusceptible of pain. Further, the optic nerve is insusceptible to the stimulus of light when severed from its connection with the retina which alone is adapted to receive luminous impressions.

The *sensation of motion* is, like motion itself, of two kinds,—progressive and vibratory. The faculty of the perception of progressive motion is possessed chiefly by the senses of vision, touch, and taste. Thus an impression is perceived travelling from one part of the retina to another, and the movement of the image is interpreted by the mind as the motion of the object. The same is the case in the sense of touch; so also the movement of a sensation of taste over the surface of the organ of taste, can be recognized. The motion of tremors, or vibrations, is perceived by several senses, but especially by those of hearing and touch.

We are made acquainted with *chemical actions* principally by taste, smell, and touch, and by each of these senses in the mode proper to it. Volatile bodies, disturbing the conditions of the nerves by a chemical action, exert the greatest influence upon the organ of smell; and many matters act on that sense which produce no impression upon the organs of taste and touch,—for example, many odorous substances, as the vapour of metals, such as lead, and the vapour of many minerals. Some volatile substances, however, are perceived not only by the sense of smell, but also by the senses of touch and taste. Thus, the vapours of horse-radish and mustard, and acrid suffocating gases, act upon the conjunctiva and the mucous membrane of the lungs, exciting through the common sensory nerves, merely modifications of common feeling; and at the same time they excite the sensations of smell and of taste.

Without simultaneous attention, all sensations are only obscurely, if at all, perceived. If the mind be torpid in indolence,

or if the attention be withdrawn from the nerves of sense in intellectual contemplation, deep speculations, or an intense passion, the sensations of the nerves make no impression upon the mind; they are not perceived,—that is to say, they are not communicated to the conscious "self," or with so little intensity, that the mind is unable to retain the impression, or only recollects it some time after, when it is freed from the preponderating influence of the idea which had occupied it.

This power of attention to the sensations derived from a single organ, may also be exercised in a single portion of a sentient organ, and thus enable one to discern the detail of what would otherwise be a single sensation. For example, by well-directed attention, one can distinguish each of the many tones simultaneously emitted by an orchestra, and can even follow the weaker tones of one instrument apart from the other sounds, of which the impressions being not attended to are less vividly perceived. So, also, if one endeavours to direct attention to the whole field of vision at the same time, nothing is seen distinctly; but when the attention is directed first to this, then to that part, and analyses the detail of the sensation, the part to which the mind is directed is perceived with more distinctness than the rest of the same sensation.

SENSE OF TOUCH.

The sense of touch is not confined to particular parts of the body of small extent, like the other senses; on the contrary, all parts capable of perceiving the presence of a stimulus by ordinary sensation are, in certain degrees, the seat of this sense; for touch is simply a modification or exaltation of common sensation or sensibility. The nerves on which the sense of touch depends are, therefore, the same as those which confer ordinary sensation on the different parts of the body, viz., those derived from the posterior roots of the nerves of the spinal cord, and the sensory cerebral nerves.

But, although all parts of the body supplied with sensory nerves are thus, in some degree, organs of touch, yet the sense is exercised in perfection only in those parts the sensibility of

which is extremely delicate, *e.g.*, the skin, the tongue, and the lips, which are provided with abundant papillæ. (See chapter on SKIN, and section on TASTE.) A peculiar and, of its own kind in each case, a very acute sense of touch is exercised through the medium of the nails and teeth. To a less extent the hair may be reckoned an organ of touch; as in the case of the eyelashes.

The sensations of the common sensory nerves have as peculiar a character as those of any other organ of sense. The sense of touch renders us conscious of the presence of a stimulus, from the slightest to the most intense degree of its action, by that indescribable something which we call feeling, or common sensation. The modifications of this sense often depend on the extent of the parts affected. The sensation of pricking, for example, informs us that the sensitive particles are intensely affected in a small extent; the sensation of pressure indicates a slighter affection of the parts in the greater extent, and to a greater depth. It is by the depth to which the parts are affected that the feeling of pressure is distinguished from that of mere contact. Schiff and Brown-Séquard are of opinion that common sensibility and tactile sensibility manifest themselves to the individual by the aid of different sets of fibres. Dr. Sieveking has arrived at the same conclusion from pathological observation.

Among the various endowments of the cutaneous surface of the body, generally included under the head of Touch, we must destinguish (*a*) the sense of *touch*, strictly so-called (tactile sensibility), (*b*) the sense of *pressure*, (*c*) the sense of *temperature*. These when carried beyond a certain degree are merged in (*d*) the sensation of *pain*.

Various peculiar sensations, such as *tickling*, must be classed with pain under the head of common sensations, since they give us no information as to external objects. Such sensations, whether pleasurable or painful, are in all cases referred by the mind to the part affected, and not to the cause which stimulates the sensory nerves of the part. The sensation of tickling may be produced in many parts of the body, but with especial intensity in the soles of the feet. Among other sensations belonging

to this class, and confined to particular parts of the body, may be mentioned those of the genital organs and nipples.

(*a*) *Touch proper.*

In almost all parts of the body which have delicate tactile sensibility the epidermis, immediately over the papillæ, is moderately thin. When its thickness is much increased, as over the heel, the sense of touch is very much dulled. On the other hand, when it is altogether removed, and the cutis laid bare, the sensation of contact is replaced by one of pain. Further, in all highly sensitive parts, the papillæ are numerous and highly vascular, and usually the sensory nerves are connected with special End-organs, End-bulbs, Pacinian bodies, or Tactile corpuscles.

The acuteness of the sense of touch depends very largely on the cutaneous circulation, which is of course largely influenced by external temperature. Hence the numbness, familiar to everyone, produced by the application of cold to the skin.

Special organs of touch are present in most animals, among which may be mentioned the antennæ of insects, the "whiskers" (vibrissæ) of cats and other carnivora, the wings of bats, the trunk of the elephant, and the hand of man.

By the sense of touch the mind is made acquainted with the size, form, and other external characters of bodies. And in order that these characters may be easily ascertained, the sense of touch is especially developed in those parts which can be readily moved over the surface of bodies. Touch, in its more limited sense, or the act of examining a body by the touch, consists merely in a voluntary employment of this sense combined with movement, and stands in the same relation to the sense of touch, or common sensibility, generally, as the act of seeking, following, or examining odours, does to the sense of smell. The hand is best adapted for it, by reason of its peculiarities of structure,—namely, its capability of pronation and supination, which enables it, by the movement of rotation, to examine the whole circumference of a body; the power it possesses of opposing the thumb to the rest of the hand; and the relative mobility of the fingers. Besides—the hand, and especially the

fingers, are abundantly endowed with *papillæ* and *touch-corpuscles* (pp. 432, 434) which are specially necessary for the perfect employment of this sense.

In forming a conception of the figure and extent of a surface, the mind multiplies the size of the hand or fingers used in the inquiry by the number of times which it is contained in the surface traversed; and by repeating this process with regard to the different dimensions of a solid body, acquires a notion of its cubical extent.

The perfection of the sense of touch on different parts of the surface is proportioned to the power which such parts possess of distinguishing and isolating the sensations produced by two points placed close together. This power depends, at least in part, on the number of primitive nerve-fibres distributed to the part; for the fewer the primitive fibres which an organ receives, the more likely is it that several impressions on different contiguous points will act on only one nervous fibre, and hence be confounded, and perhaps produce but one sensation.

Experiments to determine the tactile properties of different parts of the skin, as measured by this power of distinguishing distances, were made by E. H. Weber. The experiment consisted in touching the skin, while the eyes were closed, with the points of a pair of compasses sheathed with cork, and in ascertaining how close the points of the compasses might be brought to each other, and still be felt as two bodies. He examined in this manner nearly every part of the surface of the body, and has given tables showing the relative degrees of sensibility of different parts. Experiments of a similar kind have been performed also by Valentin.

The following table gives some of the results of Weber's experiments.

Table of variations in the tactile sensibility of different parts. The measurement indicates the least distance at which the two blunted points of a pair of compasses could be separately distinguished.

Tip of tongue	$\frac{1}{24}$ inch.
Palmar surface of third phalanx of forefinger . .	$\frac{1}{12}$,,
Palmar surface of second phalanges of fingers . .	$\frac{1}{6}$,,
Red surface of under-lip	$\frac{1}{6}$,,
Tip of the nose	$\frac{1}{4}$,,
Middle of dorsum of tongue	$\frac{1}{3}$,,
Palm of hand	$\frac{5}{12}$,,
Centre of hard palate	$\frac{1}{2}$,,
Dorsal surface of first phalanges of fingers . . .	$\frac{7}{12}$,,
Back of hand	$1\frac{1}{6}$,,

Dorsum of foot near toes	$1\frac{1}{2}$ inch.
Gluteal region	$1\frac{1}{2}$ "
Sacral region	$1\frac{1}{2}$ "
Upper and lower parts of forearm	$1\frac{1}{2}$ "
Back of neck near occiput	2 inches.
Upper dorsal and mid-lumbar regions	2 "
Middle part of forearm	$2\frac{1}{2}$ "
Middle of thigh	$2\frac{1}{2}$ "
Mid-cervical region	$2\frac{1}{2}$ "
Mid-dorsal region	$2\frac{1}{2}$ "

Moreover, in the case of the limbs, it was found that before they were recognised as two, the points of the compasses had to be *further* separated, when the line joining them was in the long axis of the limb, than when in the transverse direction. The different degrees of sensitiveness possessed by different parts may give rise to errors of judgment in estimating the distance between two points where the skin is touched. Thus, if blunted points of a pair of compasses (maintained at a constant distance apart) be slowly drawn over the skin of the cheek towards the lips, it is almost impossible to resist the conclusion that the distance between the points is gradually increasing. When they reach the lips they seem to be considerably further apart than on the cheek.

Thus, too, our estimate of the size of a cavity in a tooth is usually exaggerated when based upon sensations derived from the tongue alone.

Another curious illusion may here be mentioned. If we close the eyes, and place a small marble or pea between the crossed fore- and middle fingers, we seem to be touching two marbles. This illusion is due to an error of judgment. The marble is touched by two surfaces which, under ordinary circumstances, could only be touched by two separate marbles, hence, the mind taking no cognizance of the fact that the fingers are crossed, forms the conclusion that two sensations are due to two marbles.

According to the theory of Weber the mind estimates the distance between two points by the number of unexcited nerve-endings which intervene between the two points touched. It would appear that a certain number of intervening unexcited nerve-endings are necessary before two points touched can be

recognised as separate, and the greater this number the more clearly are the points of contact distinguished as separate. By practice the delicacy of the sense of touch may be very much increased. A familiar illustration occurs in the case of the blind, who by constant practice can acquire the power of reading raised letters the forms of which are almost if not quite undistinguishable, by the sense of touch, to an ordinary person.

The power of correctly localizing sensations of touch is gradually derived from experience. Thus infants when in pain simply cry, but make no effort to remove the cause of irritation, as an older child or adult would, doubtless on account of their imperfect knowledge of its exact situation. By long experience this power of localisation becomes perfected, till at length the brain possesses a complete "picture" as it were of the surface of the body, and is able with marvellous exactness to localise each sensation of touch.

(*b*) *Pressure.*—If the hand be rested on the table and a very light body such as a small card placed on it, the only sensation produced is one of contact; if, however, an ounce weight be laid on the card an additional sensation (that of pressure) is experienced, and this becomes more intense as the weight is increased. If now the weight be raised by the hand, we are conscious of overcoming a certain resistance; this consciousness is due to what is termed the "*muscular sense*" (p. 535).

The estimate of a weight is, therefore, usually based on *two* sensations, (1) of pressure on the skin, and (*b*) the muscular sense.

The estimate of weight derived from a combination of these two sensations (as in lifting a weight) is more accurate than that derived from the former alone (as when a weight is laid on the hand); thus Weber found that by the former method he could generally distinguish 19½ oz. from 20 oz., but not 19¾ oz. from 20, while by the latter he could at most only distinguish 14½ oz. from 15 oz.

It is not the absolute, but the relative, amount of the difference of weight which we have thus the faculty of perceiving.

It is not, however, certain, that our idea of the amount of muscular force used is derived solely from sensation in the muscles. We have the power of estimating very accurately beforehand, and of regulating, the amount of

nervous influence necessary for the production of a certain degree of movement. When we raise a vessel, with the contents of which we are not acquainted, the force we employ is determined by the idea we have conceived of its weight. If it should happen to contain some very heavy substance, as quicksilver, we shall probably let it fall; the amount of muscular action, or of nervous energy, which we had exerted being insufficient. The same thing occurs sometimes to a person descending stairs in the dark; he makes the movement for the descent of a step which does not exist. It is possible that in the same way the idea of weight and pressure in raising bodies, or in resisting forces, may in part arise from a consciousness of the amount of nervous energy transmitted from the brain rather than from a sensation in the muscles themselves. The mental conviction of the inability longer to support a weight must also be distinguished from the actual sensation of fatigue in the muscles.

So, with regard to the ideas derived from sensations of touch combined with movements, it is doubtful how far the consciousness of the extent of muscular movement is obtained from sensations in the muscles themselves. The sensation of movement attending the motions of the hand is very slight; and persons who do not know that the action of particular muscles is necessary for the production of given movements, do not suspect that the movement of the fingers, for example, depends on an action in the forearm. The mind has, nevertheless, a very definite knowledge of the changes of position produced by movements; and it is on this that the ideas which it conceives of the extension and form of a body are in great measure founded.

(*c*) *Temperature.*—The whole surface of the body is more or less sensitive to differences of temperature. The sensation of heat is as distinct from that of touch as the pitch of a sound is from its intensity; and it would seem reasonable to suppose that there are special nerves and nerve-endings for temperature, distinct from those of touch. At any rate the power of discriminating temperature may remain unimpaired when the sense of touch is temporarily in abeyance. Thus if the ulnar nerve be compressed at the elbow till the sense of touch is very much dulled in the fingers which it supplies, the sense of temperature remains quite unaffected (Nothnagel).

The sensations of heat and cold are often exceedingly fallacious, and in many cases are no guide at all to the absolute temperature as indicated by a thermometer. All that we can with safety infer from our sensations of temperature, is that a given object is warmer or cooler than the skin. Thus the temperature of our own skin is the standard; and as this varies from hour to hour according to the activity of the cutaneous

circulation, our estimate of the absolute temperature of any body must necessarily vary too. If we put the left hand into water at 40° F. and the right into water at 110° F., and then immerse both in water at 80° F., it will feel warm to the left hand but cool to the right. Again a piece of metal which has really the same temperature as a given piece of wood will feel much colder, since it conducts away the heat much more rapidly. For the same reason air in motion feels very much cooler than air of the same temperature at rest.

Perhaps the most striking example of the fallaciousness of our sensations as a measure of temperature is afforded by fever. In a shivering fit of ague the patient feels excessively cold, whereas his actual temperature is several degrees above the normal, while in the sweating stage which succeeds it he feels very warm, whereas really his temperature has fallen several degrees. In the former case the cutaneous circulation is much diminished, in the latter much increased; hence the sensations of cold and heat respectively.

In some cases we are able to form a fairly accurate estimate of absolute temperature. Thus, by plunging the elbow into a bath, a practised bath-attendant can tell the temperature sometimes within 1° F.

The temperatures which can be readily discriminated are between 50° F. and 115° F.; very low and very high temperatures alike produce a burning sensation. A temperature appears higher according to the extent of cutaneous surface exposed to it. Thus, water of a temperature which can be readily borne by the hand, is quite intolerable if the whole body be immersed. So, too, water appears much hotter to the hand than to a single finger. In this way Weber found that water at 97° F. felt positively warmer to the *hand*, than water at 104° F. to the *finger*.

The delicacy of the sense of temperature coincides in the main with that of touch, and appears to depend largely on the thickness of the skin; hence, in the elbow where the skin is thin, the sense of temperature is delicate, though that of touch is not remarkably so. Weber has further ascertained the following

facts: two compass points so near together on the skin that they produce but a single impression, at once give rise to *two* sensations, when one is hotter than the other. Moreover, of two bodies of equal weight, that which is the colder feels heavier than the other.

As every sensation is attended with an idea, and leaves behind it an idea in the mind which can be reproduced at will, we are enabled to compare the idea of a past sensation with another sensation really present. Thus we can compare the weight of one body with another which we had previously felt, of which the idea is retained in our mind. Weber was indeed able to distinguish in this manner between temperatures, experienced one after the other, better than between temperatures to which the two hands were simultaneously subjected. This power of comparing present with past sensations diminishes, however, in proportion to the time which has elapsed between them.

The *after-sensations* left by impressions on nerves of common sensibility or touch are very vivid and durable. As long as the condition into which the stimulus has thrown the organ endures, the sensation also remains, though the exciting cause should have long ceased to act. Both painful and pleasurable sensations afford many examples of this fact.

Subjective sensations, or sensations dependent on internal causes, are in no sense more frequent than in the sense of touch. All the sensations of pleasure and pain, of heat and cold, of lightness and weight, of fatigue, etc., may be produced by internal causes. Neuralgic pains, the sensation of rigor, formication or the creeping of ants, and the states of the sexual organs occurring during sleep, afford striking examples of subjective sensations.

The mind has a remarkable power of exciting sensations in the nerves of common sensibility; just as the thought of the nauseous excites sometimes the sensation of nausea, so the idea of pain gives rise to the actual sensation of pain in a part predisposed to it. A painful sensation becomes more intolerable the more the attention is directed to it: thus, a sensation in itself inconsiderable, as an itching in a very small spot of the

skin, may be rendered very troublesome and enduring. The thought of anything horrid excites the sensation of shuddering; the feelings of eager expectation, of pathetic emotion, of enthusiasm, excite in some persons a sensation of "concentration" at the top of the head, and of cold trickling through the body; fright causes sensations to be felt in many parts of the body; and even the thought of tickling excites that sensation in individuals very susceptible of it, when they are threatened with it by the movements of another person. These sensations from internal causes are most frequent in persons of excitable nervous systems, such as the hypochondriacal and the hysterical, of whom it is usual to say that their pains are imaginary. If by this is meant that their pains exist in their imagination merely, it is certainly quite incorrect. Pain is never imaginary in this sense; but is as truly pain when arising from internal as from external causes; the idea of pain only can be unattended with sensation, but of the mere idea no one will complain. Still, it is quite certain that the imagination can render pain that already exists more intense, and can excite it when there is a disposition to it.

SENSE OF TASTE.

The conditions for the perception of taste are:—1, the presence of a nerve and nerve-centre with special endowments; 2, the excitation of the nerves by the sapid matters, which for this purpose must be in a state of solution. The nerves concerned in the production of the sense of taste have been already considered (pp. 563 and 567).

The mode of action of the substances which excite taste probably consists in the production of a change in the condition of the gustatory nerves; and, according to the difference of the substances, an infinite variety of changes of condition of the nerves, and consequently of stimulations of the gustatory centre, may be induced. The matters to be tasted must either be in solution or be soluble in the moisture covering the tongue; hence insoluble substances are usually tasteless, and produce merely sensations of touch. Moreover, for the perfect action of

a sapid, as of an odorous substance, it is necessary that the sentient surface should be moist. Hence, when the tongue and fauces are dry, sapid substances, even in solution, are with difficulty tasted.

The nerves of taste, like the nerves of other special senses, may have their peculiar properties excited by various other kinds of irritation, such as electricity and mechanical impressions. Thus, Henle observed that a small current of air directed upon the tongue gives rise to a cool saline taste, like that of saltpetre; and Dr. Baly has shown that a distinct sensation of taste, similar to that caused by electricity, may be produced by a smart tap applied to the papillæ of the tongue. Moreover, the mechanical irritation of the fauces and palate produces the sensation of nausea, which is probably only a modification of taste.

The principal, but not exclusive seat of the sense of taste is the fauces and tongue.

The Tongue is a muscular organ covered by mucous membrane.

The muscles, which form the greater part of the substance of the tongue (*intrinsic* muscles) are termed *linguales*; and by these, which are attached to the mucous membrane chiefly, its smaller and more delicate movements are chiefly performed.

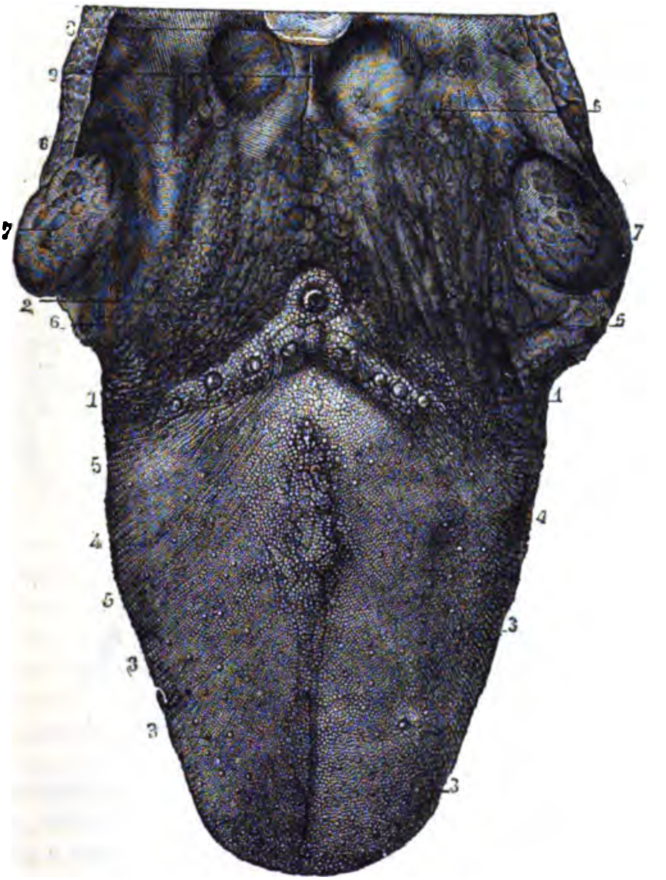
By other muscles (*extrinsic* muscles) as the genio-hyoglossus the styloglossus, etc., the tongue is fixed to surrounding parts; and by this group of muscles its larger movements are performed.

The mucous membrane of the tongue resembles other mucous membranes (p. 411) in essential points of structure, but contains *papillæ*, more or less peculiar to itself; peculiar, however, in details of structure and arrangement, not in their nature. The tongue is beset with numerous mucous follicles and glands. The use of the tongue in relation to mastication and deglutition has already been considered (pp. 283 and 294).

The larger *papillæ* of the tongue are thickly set over the anterior two-thirds of its upper surface, or *dorsum* (fig. 285), and give to it its characteristic roughness. In Carnivorous animals, especially those of the cat tribe, the papillæ attain a large size, and are developed into sharp recurved horny spines. Such papillæ cannot be regarded as sensitive, but they enable the tongue to

play the part of a most efficient rasp, as in scraping bones, or of a comb in cleaning their fur. Their greater prominence than those

*Fig. 285.**



* Fig. 285. Papillar surface of the tongue, with the fauces and tonsils (from Sappey).—1, 1, circumvallate papillæ, in front of 2, the foramen cæcum; 3, fungiform papillæ; 4, filiform and conical papillæ; 5, transverse and oblique rugæ; 6, mucous glands at the base of the tongue and in the fauces; 7, tonsils; 8, part of the epiglottis; 9, median glosso-epiglottidean fold (frænum epiglottidis).

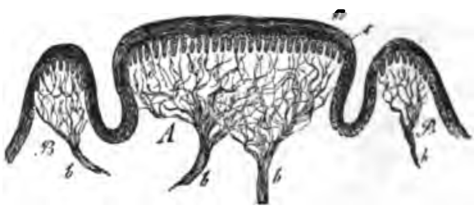
of the skin is due to their interspaces not being filled up with epithelium, as the interspaces of the papillæ of the skin are. The papillæ of the tongue present several diversities of form; but three principal varieties, differing both in seat and general characters, may usually be distinguished, namely, the *circumvallate* or *calyciform*, the *fungiform*, and the *filiform* papillæ. Essentially these have all of them the same structure, that is to say, they are all formed by a projection of the mucous membrane, and contain special branches of blood-vessels and nerves. In details of structure, however, they differ considerably one from another.

The surface of each kind is studded by minute conical processes of mucous membrane, which thus form secondary papillæ. (Todd and Bowman).

Secondary papillæ also occur over most other parts of the tongue not occupied by the compound papillæ, and extend for some distance behind the papillæ circumvallatæ. The mucous membrane immediately in front of the epiglottis is, however, free from them. They are commonly buried beneath the epithelium; hence they are often overlooked.

Circumvallate or Calyciform Papillæ.—These papillæ (fig. 286),

Fig. 286.*



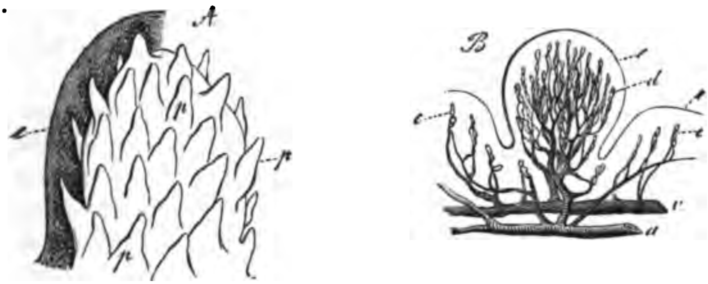
eight or ten in number, are situate in two V-shaped lines at the base of the tongue (1, 1, fig. 285). They are circular elevations from $\frac{1}{20}$th to $\frac{1}{12}$th of an inch wide, each with a central depression, and surrounded by a circular fissure, at the outside of which again is a slightly elevated ring, both the central

* Fig. 286. Vertical section of the circumvallate papillæ $\frac{10}{1}$.—A, he a-pillæ; B, the surrounding wall; *a*, the epithelial covering; *b*, the nerves of the papilla and wall spreading towards the surface; *c*, the secondary papillæ (Kölliker).

elevation and the ring being formed of close set simple papillæ (fig. 286).

Fungiform Papillæ.—The fungiform papillæ (3, fig. 285) are scattered chiefly over the sides and tip, and sparingly over the middle of the dorsum, of the tongue; their name is derived from their being usually narrower at their base than at their summit. They also consist of groups of simple papillæ (A. fig. 287), each of which contains in its interior a loop of capillary blood-vessels (B.), and a nerve-fibre.

Fig. 287.*



Conical or Filiform Papillæ.—These, which are the most abundant papillæ, are scattered over the whole surface of the tongue, but especially over the middle of the dorsum (fig. 285).

They vary in shape somewhat, but for the most part are conical or filiform, and covered by a thick layer of epidermis, which is arranged over them, either in an imbricated manner, or is prolonged from their surface in the form of fine stiff projections, hair-like in appearance, and in some instances in structure also (fig. 288). From their peculiar structure, it seems likely that these papillæ have a mechanical function, or one allied to that of touch rather than of taste; the latter sense

* Fig. 287. Surface and section of the fungiform papillæ (from Kölliker, after Todd and Bowman).—A, the surface of a fungiform papilla, partially denuded of its epithelium, Y; *p*, secondary papillæ; *e*, epithelium. B, section of a fungiform papilla with the blood-vessels injected; *a*, artery; *v*, vein; *c*, capillary loops of simple papillæ in the neighbouring structure of the tongue; *d*, capillary loops of the secondary papillæ; *e*, epithelium.

being probably seated especially in the other two varieties of papillæ, the *circumvallate* and the *fungiform*.

The *epithelium* of the tongue is of the squamous kind. It covers every part of the surface; but over the fungiform papillæ forms a thinner layer than elsewhere. The epithelium covering the filiform papillæ has been shown by Todd and Bowman, to have a singular arrangement; being extremely dense and thick, and, as before mentioned, projecting from their sides and summits in the form of long, stiff, hair-like processes (fig. 288). Many of these processes bear a close resemblance to hairs, and some actually contain minute hair-tubes. Blood-vessels and nerves are supplied freely to the papillæ. The nerves in the fungiform and circumvallate papillæ form a kind of plexus, spreading out brush-wise (fig. 286), but the exact mode of termination of the nerve filaments is not certainly known.

Fig. 288.*

In the circumvallate papillæ of the tongue of man peculiar structures, known as gustatory buds or taste-goblets, have been

* Fig. 288. Two filiform papillæ, one with epithelium, the other without (from Kölliker, after Todd and Bowman). ¥.—*p*, the substance of the papillæ dividing at their upper extremities into secondary papillæ; *a*, artery, and *v*, vein, dividing into capillary loops; *e*, epithelial covering, laminated between the papillæ, but extended into hair-like processes, *f*, from the extremities of the secondary papillæ.

discovered (Lóven, Schwalbe). They are of an oval shape, and consist of a number of closely packed, very narrow and fusiform, cells (*gustatory cells*). This central core of gustatory cells is enclosed in a single layer of broader fusiform cells (*encasing cells*). The gustatory cells terminate in fine spikes not unlike cilia, which project on the free surface (fig. 289).

Fig. 289.*

These bodies also occur side by side in considerable numbers in the epithelium of a foliated body ("papilla foliata"), which is situated near the root of the tongue in the rabbit, and also in man. Similar "taste-goblets" also occur pretty evenly distributed on the posterior (laryngeal) surface of the epiglottis (Verson, Schofield). It seems probable, from their distribution, that all these so-called taste-geblets are gustatory in function, though no nerves have been distinctly traced into them.

The tongue is not the only seat of the sense of taste; for the results of experiments as well as ordinary experience show that the soft palate and its arches, the uvula, tonsils, and probably the upper part of the pharynx, are endowed with taste. These parts, together with the base and posterior parts of the tongue, are supplied with branches of the glosso-pharyngeal nerve, and evidence has been already adduced that the sense of taste is conferred upon them by this nerve.

In most, though not in all persons, the anterior parts of the tongue, especially the edges and tip, are endowed with the

* Fig. 289. Taste-goblet from dog's epiglottis (laryngeal surface near the base), precisely similar in structure to those found in the tongue. *a*, depression in epithelium over goblet; below the letter are seen the fine hair-like processes in which the cells terminate; *c*, two nuclei of the axial (gustatory) cells. The more superficial nuclei belong to the superficial (encasing) cells; the converging lines indicate the fusiform shape of the encasing cells. × 400 (Schofield).

sense of taste. The middle of the dorsum is only feebly endowed with this sense, probably because of the density and thickness of the epithelium covering the filiform papillæ of this part of the tongue, which will prevent the sapid substances from penetrating to their sensitive parts. The gustatory property of the anterior part of the tongue is due, as already said (p. 568), to the lingual or gustatory branch of the fifth nerve.

Besides the sense of taste, the tongue, by means also of its papillæ, is endued, especially at its sides and tip, with a very delicate and accurate sense of touch (p. 637), which renders it sensible of the impressions of heat and cold, pain and mechanical pressure, and consequently of the form of surfaces. The tongue may lose its common sensibility, and still retain the sense of taste, and *vice versâ*. This fact renders it probable that, although the senses of taste and of touch may be exercised by the same papillæ supplied by the same nerves, yet the nervous conductors for these two different sensations are distinct, just as the nerves for smell and common sensibility in the nostrils are distinct; and it is quite conceivable that the same nervous trunk may contain fibres differing essentially in their specific properties. Facts already detailed (p. 568) seem to prove that the lingual branch of the fifth nerve is the conductor of sensations of taste in the anterior part of the tongue; and it is also certain, from the marked manifestations of pain to which its division in animals gives rise, that it is likewise a nerve of common sensibility. The glosso-pharyngeal also seems to contain fibres both of common sensation and of the special sense of taste.

The concurrence of common and special sensibility in the same part makes it sometimes difficult to determine whether the impression produced by a substance is perceived through the ordinary sensitive fibres, or through those of the sense of taste. In many cases, indeed, it is probable that both sets of nerve-fibres are concerned, as when irritating acrid substances are introduced into the mouth.

Much of the perfection of the sense of taste is often due to the sapid substances being also odorous, and exciting the simultaneous action of the sense of smell. This is shown by the imperfec-

tion of the taste of such substances when their action on the olfactory nerves is prevented by closing the nostrils. Many fine wines lose much of their apparent excellence if the nostrils are held close while they are drunk.

Among the most clearly defined tastes are the sweet and bitter (which are more or less opposed to each other), the acid, alkaline, and saline tastes. Acid and alkaline taste may be excited by electricity. If a piece of zinc be placed beneath and a piece of copper above the tongue, and their ends brought into contact, an acid taste (due to the feeble galvanic current) is produced.

The delicacy of the sense of taste is sufficient to discern 1 part of sulphuric acid in 1000 of water; but it is far surpassed in acuteness by the sense of smell.

Very distinct sensations of taste are frequently left after the substances which excited them have ceased to act on the nerve; and such sensations often endure for a long time, and modify the taste of other substances applied to the tongue afterwards. Thus, the taste of sweet substances spoils the flavour of wine, the taste of cheese improves it. There appears, therefore, to exist the same relation between tastes as between colours, of which those that are opposed or complementary render each other more vivid, though no general principles governing this relation have been discovered in the case of tastes. In the art of cooking, however, attention has at all times been paid to the consonance or harmony of flavours in their combination or order of succession, just as in painting and music the fundamental principles of harmony have been employed empirically while the theoretical laws were unknown.

Frequent and continued repetitions of the same taste render the perception of it less and less distinct, in the same way that a colour becomes more and more dull and indistinct the longer the eye is fixed upon it. Thus, after frequently tasting first one and then the other of two kinds of wine, it becomes impossible to discriminate between them.

The simple contact of a sapid substance with the surface of the gustatory organ seldom gives rise to a distinct sensation of

taste; it needs to be diffused over the surface, and brought into intimate contact with the sensitive parts by compression, friction, and motion between the tongue and palate.

The sense of taste seems capable of being excited also by internal causes, such as changes in the conditions of the nerves or nerve-centres, produced by congestion or other causes, which excite subjective sensations in the other organs of sense. But little is known of the subjective sensations of taste; for it is difficult to distinguish the phenomena from the effects of external causes, such as changes in the nature of the secretions of the mouth.

THE SENSE OF SMELL.

The sense of smell ordinarily requires, for its excitement to a state of activity, the action of external matters, which action produces certain changes in the olfactory nerve; and this nerve is susceptible of an infinite variety of states dependent on the nature of the external stimulus.

The first conditions essential to the sense of smell are a special *nerve* and *nerve-centre*, the changes in whose condition are perceived in sensations of odour; for no other nervous structure is capable of these sensations, even though acted on by the same causes. The same substance which excites the sensation of smell in the olfactory centre may cause another peculiar sensation through the nerves of taste, and may produce an irritating and burning sensation on the nerves of touch; but the sensation of odour is yet separate and distinct from these, though it may be simultaneously perceived. The second condition of smell is a peculiar change produced in the olfactory nerve and its centre by the stimulus or odorous substance.

The material causes of odours are, usually, in the case of animals living in the air, either solids suspended in a state of extremely fine division in the atmosphere; or gaseous exhalations often of so subtile a nature that they can be detected by no other re-agent than the sense of smell itself. The matters of odour must, in all cases, be dissolved in the mucus of the mucous membrane before they can be immediately applied to, or affect the olfactory nerves; therefore a further condition necessary for

the perception of odours is, that the mucous membrane of the nasal cavity be moist. When the Schneiderian membrane is dry, the sense of smell is impaired or lost; in the first stage of catarrh, when the secretion of mucus within the nostrils is lessened, the faculty of perceiving odour is either lost, or rendered very imperfect.

In animals living in the air, it is also requisite that the odorous matter should be transmitted in a current through the nostrils. This is effected by an inspiratory movement, the mouth being closed; hence we have voluntary influence over the sense of smell; for by interrupting respiration we prevent the perception of odours, and by repeated quick inspiration, assisted, as in the act of *sniffing*, by the action of the nostrils, we render the impression more intense (see p. 256).

An odorous substance in a liquid form injected into the nostrils appears incapable of giving rise to the sensation of smell: thus Weber could not smell the slightest odour when his nostrils were completely filled with water containing a large quantity of eau de Cologne.

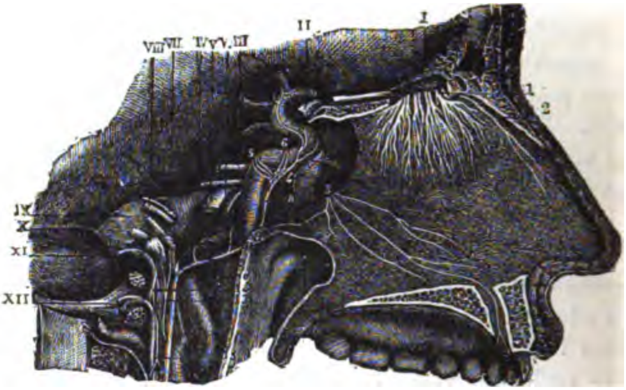
The human organ of smell is formed by the filaments of the olfactory nerves, distributed in the mucous membrane covering the upper third of the septum of the nose, the superior turbinated or spongy bone, the upper part of the middle turbinated bone, and the upper wall of the nasal cavities beneath the cribriform plates of the ethmoid bones (figs. 290 and 291).

The olfactory region is covered by cells of *cylindrical* epithelium, prolonged at their deep extremities into fine branched processes, but not ciliated; and interspersed with these are fusiform (*olfactory*) cells, with both superficial and deep processes (fig. 292), the latter being probably connected with the terminal filaments of the olfactory nerve. The lower, or *respiratory* part, as it is called, of the nasal fossæ is lined by *cylindrical ciliated* epithelium, except in the region of the nostrils, where it is *squamous*.

The branches of the olfactory nerves retain much of the same soft and greyish texture which distinguishes those of the olfactory *tracts* within the cranium. Their filaments, also, are

peculiar, more resembling those of the sympathetic nerve than the filaments of the other cerebral nerves do, containing no outer white substance, and being finely granular and nucleated.

Fig. 290.*



The sense of smell is derived exclusively through those parts of the nasal cavities in which the olfactory nerves are distributed; the accessory cavities or sinuses communicating with the nostrils seem to have no relation to it. Air impregnated with the vapour of camphor was injected by Deschamps into the frontal sinus through a fistulous opening, and Richerand injected odorous substances into the antrum of Highmore; but in neither case was any odour perceived by the patient. The purposes of these sinuses appear to be, that the bones, necessarily large for the action of the muscles and other parts connected with them, may be as light as possible, and that there may be more room for the resonance of the air in vocalising. The former purpose, which is in other bones obtained by filling their cavities with fat, is here attained, as it is in many bones of birds, by their being filled with air.

All parts of the nasal cavities, whether or not they can be the seats of the sense of smell, are endowed with common sensibility by the nasal branches of the first and second divisions of the fifth nerve. Hence the sensations of cold, heat, itching, tickling, and pain; and the sensation of tension or pressure in the nostrils. That these nerves cannot perform the function of the olfactory

* Fig. 290. Nerves of the septum nasi, seen from the right side. ⅜.—I, the olfactory bulb; 1, the olfactory nerves passing through the foramina of the cribriform plate, and descending to be distributed on the septum; 2, the internal or septal twig of the nasal branch of the ophthalmic nerve; 3, naso-palatine nerves (from Sappey, after Hirschfeld and Leveillé).

nerves is proved by cases in which the sense of smell is lost, while the mucous membrane of the nose remains susceptible of the various modifications of common sensation or touch. But it

Fig. 291.*

Fig. 292.†

is often difficult to distinguish the sensation of smell from that of mere feeling, and to ascertain what belongs to each separately. This is the case particularly with the sensations excited in the nose by acrid vapours, as of ammonia, horse-radish, mustard, etc., which resemble much the sensations of the nerves of touch; and the difficulty is the greater, when it is remembered that these acrid vapours have nearly the same action upon the mucous

* Fig. 291. Nerves of the outer walls of the nasal fossæ. ½.—1, network of the branches of the olfactory nerve, descending upon the region of the superior and middle turbinated bones; 2, external twig of the ethmoidal branch of the nasal nerves; 3, spheno-palatine ganglion; 4, ramification of the anterior palatine nerves; 5, posterior, and 6, middle divisions of the palatine nerves; 7, branch to the region of the inferior turbinated bone; 8, branch to the region of the superior and middle turbinated bones; 9, naso-palatine branch to the septum cut short (from Sappey, after Hirschfeld and Leveillé).

† Fig. 292. Epithelial and olfactory cells of man. The letters are placed on the free surface. *E, E*, epithelial cells; *Olf.*, olfactory cells. (Max Schultze.)

membrane of the eyelids. It was because the common sensibility of the nose to these irritating substances remained after the destruction of the olfactory nerves, that Magendie was led to the erroneous belief that the fifth nerve might exercise this special sense.

Animals do not all equally perceive the same odours; the odours most plainly perceived by an herbivorous animal and by a carnivorous animal are different. The Carnivora have the power of detecting most accurately by the smell the special peculiarities of animal matters, and of tracking other animals by the scent; but have apparently very little sensibility to the odours of plants and flowers. Herbivorous animals are peculiarly sensitive to the latter, and have a narrower sensibility to animal odours, especially to such as proceed from other individuals than their own species. Man is far inferior to many animals of both classes in respect of the acuteness of smell; but his sphere of susceptibility to various odours is more uniform and extended. The cause of this difference lies probably in the endowments of the cerebral parts of the olfactory apparatus.

The delicacy of the sense of smell is most remarkable; it can discern the presence of bodies in quantities so minute as to be undiscoverable even by spectrum analysis; $\frac{3}{100,000,000}$ of a grain of musk can be distinctly smelt (Valentin).

Opposed to the sensation of an agreeable odour is that of a disagreeable or disgusting odour, which corresponds to the sensations of pain, dazzling and disharmony of colours, and dissonance in the other senses. The cause of this difference in the effect of different odours is unknown; but this much is certain, that odours are pleasant or offensive in a relative sense only, for many animals pass their existence in the midst of odours which to us are highly disagreeable. A great difference in this respect is, indeed, observed amongst men: many odours, generally thought agreeable, are to some persons intolerable; and different persons describe differently the sensations that they severally derive from the same odorous substances. There seems also to be in some persons an insensibility to certain odours, comparable with that of the eye to certain colours; and among different persons, as

great a difference in the acuteness of the sense of smell as among others in the acuteness of sight. We have no exact proof that a relation of harmony and disharmony exists between odours as between colours and sounds; though it is probable that such is the case, since it certainly is so with regard to the sense of taste; and since such a relation would account in some measure for the different degrees of perceptive power in different persons; for as some have no ear for music (as it is said), so others have no clear appreciation of the relation of odours, and therefore little pleasure in them.

The sensations of the olfactory nerves, independent of the external application of odorous substances, have hitherto been little studied. The friction of the electric machine produces a smell like that of phosphorus. Ritter, too, has observed, that when galvanism is applied to the organ of smell, besides the impulse to sneeze, and the tickling sensation excited in the filaments of the fifth nerve, a smell like that of ammonia was excited by the negative pole, and an acid odour by the positive pole, whichever of these sensations were produced, it remained constant as long as the circle was closed, and changed to the other at the moment of the circle being opened. *Subjective* sensations occur frequently in connection with the sense of smell. Frequently a person smells something which is not present, and which other persons cannot smell; this is very frequent with nervous people, but it occasionally happens to every one. In a man who was constantly conscious of a bad odour, the arachnoid was found after death, by MM. Cullerier and Maignault, to be beset with deposits of bone; and in the middle of the cerebral hemispheres were scrofulous cysts in a state of suppuration. Dubois was acquainted with a man who, ever after a fall from his horse, which occurred several years before his death, believed that he smelt a bad odour.

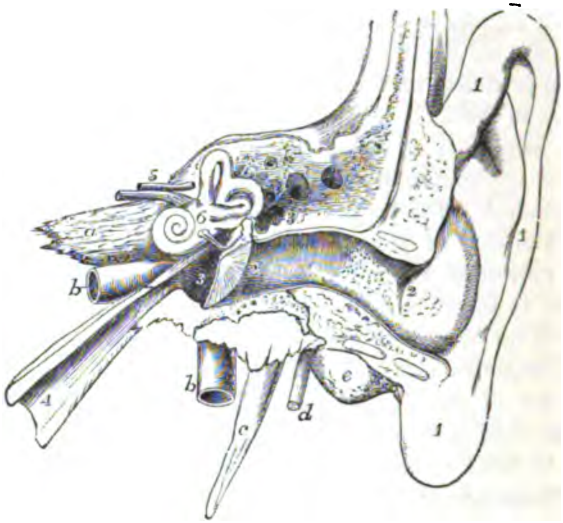
SENSE OF HEARING.

Anatomy of the Organ of Hearing.

For descriptive purposes, the Ear, or organ of Hearing, is divided into three parts, the *external*, the *middle*, and the *internal*

ear. The two first are only accessory to the third or internal ear, which contains the essential parts of an organ of hearing. The accompanying figure shows very well the relation of these divisions,—one to the other (fig. 293).

Fig. 293.*



External Ear.—The external ear consists of the *pinna* or *auricle*, and the external *auditory canal* or *meatus*.

* Fig. 293. Diagrammatic view from before of the parts composing the organ of hearing of the left side (Arnold). The temporal bone of the left side, with the accompanying soft parts, has been detached from the head, and a section has been carried through it transversely, so as to remove the front of the meatus externus, half the tympanic membrane, the upper and anterior wall of the tympanum and Eustachian tube. The meatus internus has also been opened, and the bony labyrinth exposed by the removal of the surrounding parts of the petrous bone. 1. the pinna and lobe ; 2, 2′, meatus externus ; 2′, membrana tympani ; 3, cavity of the tympanum ; 3′, its opening backwards into the mastoid cells ; between 3 and 3′, the chain of small bones ; 4, Eustachian tube ; 5, meatus internus, containing the facial (uppermost) and the auditory nerves ; 6, placed on the vestibule of the labyrinth above the fenestra ovalis : *a*, apex of the petrous bone ; *b*, internal carotid artery ; *c*, styloid process ; *d*, facial nerve issuing from the stylo-mastoid foramen ; *e*, mastoid process ; *f*, squamous part of the bone covered by integument, etc.

The principal parts of the *pinna* (fig. 294) are two prominent rims enclosed one within the other (*helix* and *antihelix*), and enclosing a central hollow named the *concha;* in front of the concha, a prominence directed backwards, the *tragus*, and opposite to this, one directed forwards, the *antitragus*. From the concha, the auditory canal, with a slight arch directed upwards, passes inwards and a little forwards to the membrana tympani, to which it thus serves to convey the vibrating air. Its outer part consists of fibro-cartilage continued from the concha; its inner part of bone. Both are lined by skin continuous with that of the pinna, and extending over the outer part of the *membrana tympani*.

Fig. 294.*

Towards the outer part of the canal are fine hairs and sebaceous glands, while deeper in the canal are small glands, resembling the sweat-glands in structure, which secrete a peculiar yellow substance called *cerumen*, or ear-wax.

Middle Ear or Tympanum.—The *middle* ear, or *tympanum* (3, fig. 293) is separated by the *membrana tympani* from the external auditory canal. It is a cavity in the temporal bone, opening through its anterior and inner wall into the Eustachian tube, a cylindriform flattened canal, dilated at both ends, composed partly of bone and partly of cartilage, and lined with mucous membrane, which forms a communication between the tympanum and the pharynx. It opens into the cavity of the pharynx just behind the posterior aperture of the nostrils. The cavity of the tympanum communicates posteriorly with air-cavities, the *mastoid cells* in the mastoid process of the temporal bone; but its only opening to the external air is through the Eustachian tube (4, fig. 293). The walls of the tympanum are osseous, except where apertures in them are closed with membrane, as at the fenestra rotunda, and fenestra ovalis, and at the outer part where the bone is replaced by the *membrana tympani*. The cavity of the tympanum is lined with mucous membrane, the epithelium of which is

* Fig. 294. Outer surface of the pinna of the right auricle. ⅓.—1, helix; 2, fossa of the helix; 3, antihelix; 4, fossa of the antihelix; 5, antitragus; 6, tragus; 7, concha; 8, lobule.

ciliated and continuous with that of the pharynx. It contains a chain of small bones (*ossicula auditus*), which extends from the membrana tympani to the fenestra ovalis.

The *membrana tympani* is placed in a slanting direction at the bottom of the external auditory canal, its plane being at an angle of about 45° with the lower wall of the canal. It is formed chiefly of a tough and tense fibrous membrane, the edges of which are set in a bony groove; its outer surface is covered with a continuation of the cutaneous lining of the auditory canal, its inner surface with part of the ciliated mucous membrane of the tympanum.

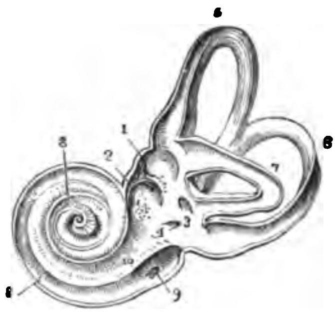
The small bones or *ossicles* of the ear are three, named *malleus*, *incus*, and *stapes*. The *malleus*, or hammer-bone, is attached by a long slightly-curved process, called its handle, to the membrana tympani; the line of attachment being vertical, including the whole length of the handle, and extending from the upper border to the centre of the membrane. The head of the malleus is irregularly rounded; its neck, or the line of boundary between it and the handle, supports two processes; a *short* conical one, which receives the insertion of the *tensor tympani*, and a *slender* one, *processus gracilis*, which extends forwards, and to which the *laxator tympani* muscle is attached. The *incus*, or anvil-bone, shaped like a bicuspid molar tooth, is articulated by its broader part, corresponding with the surface of the crown of a tooth, to the malleus. Of its two fang-like processes, one, directed backwards, has a free end lodged in a depression in the mastoid bone; the other, curved downwards and more pointed, articulates by means of a roundish tubercle, formerly called *os orbiculare*, with the stapes, a little bone shaped exactly like a stirrup, of which the base or bar fits into the fenestra ovalis. To the neck of the stapes, a short process, corresponding with the loop of the stirrup, is attached the *stapedius* muscle.

The bones of the ear are covered with mucous membrane reflected over them from the wall of the tympanum; and are moveable both altogether and one upon the other. The malleus moves and vibrates with every movement and vibration of the membrana tympani, and its movements are communicated through the incus to the stapes, and through it to the membrane closing the fenestra ovalis. The malleus, also, is moveable in its articulation with the incus; and the membrana tympani moving with it is altered in its degree of tension by the laxator and tensor tympani muscles. The stapes is moveable on the process of the incus, when the stapedius muscle acting, draws it backwards. The axis round which the malleus and incus rotate is the line joining the processus gracilis of the malleus and the posterior (short) process of the incus.

Internal Ear.—The proper organ of hearing is formed by the distribution of the auditory nerve within the *internal ear*, or *labyrinth* of the ear, a set of cavities within the petrous portion of the temporal bone.] The bone which forms the walls of these

Fig. 295.*

Fig. 296.†



cavities is denser than that around it, and forms the *osseous labyrinth;* the membrane within the cavities forms the *membranous labyrinth.* The membranous labyrinth contains a fluid called *endolymph;* while outside it, between it and the osseous labyrinth, is a fluid called *perilymph.*

The osseous labyrinth consists of three principal parts, namely, the *vestibule*, the *cochlea*, and the *semicircular canals.*

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* Fig. 295. Right bony labyrinth, viewed from the outer side (Sömmerring). $\frac{2\frac{1}{2}}{1}$.—The specimen here represented is prepared by separating piecemeal the looser substance of the petrous bone from the dense walls which immediately enclose the labyrinth. 1, the vestibule; 2, fenestra ovalis; 3, superior semicircular canal; 4, horizontal or external canal; 5, posterior canal; *, ampullæ of the semicircular canals; 6, first turn of the cochlea; 7, second turn; 8, apex; 9, fenestra rotunda. The smaller figure in outline below shows the natural size.

† Fig. 296. View of the interior of the left labyrinth (Sömmerring). $\frac{2\frac{1}{2}}{1}$.—The bony wall of the labyrinth is removed superiorly and externally. 1, fovea hemielliptica; 2, fovea hemispherica; 3, common opening of the superior and posterior semicircular canals; 4, opening of the aqueduct of the vestibule; 5, the superior, 6, the posterior, and 7, the external semicircular canals; 8, spiral tube of the cochlea (scala tympani); 9, opening of the aqueduct of the cochlea; 10, placed on the lamina spiralis in the scala vestibuli.

The vestibule is the middle cavity of the labyrinth, and the central organ of the whole auditory apparatus. It presents, in its inner wall, several openings for the entrance of the divisions of the auditory nerve ; in its outer wall, the *fenestra ovalis* (2, fig. 295), an opening filled by the base of the *stapes*, one of the small bones of the ear ; in its posterior and superior walls, five openings by which the *semicircular canals* communicate with it : in its anterior wall, an opening leading into the *cochlea*. The hinder part of the inner wall of the vestibule also presents an opening, the orifice of the *aquæductus vestibuli*, a canal leading to the posterior margin of the petrous bone, with uncertain contents and unknown purpose.

The *semicircular canals* (figs. 295, 296) are three arched cylindriform bony canals, set in the substance of the petrous bone. They all open at both ends into the vestibule (two of them first coalescing). The ends of each are dilated just before opening into the vestibule ; and one end of each being more dilated than the other is called an *ampulla*. Two of the canals form nearly vertical arches ; of these the superior is also anterior ; the posterior is inferior ; the third canal is horizontal, and lower and shorter than the others.

The *cochlea* (6, 7, 8, fig. 295 and fig. 297), a small organ, shaped like a common snail-shell, is seated in front of the vestibule, its base resting on the bottom of the internal meatus, where some apertures transmit to it the cochlear filaments of the auditory nerve. In its axis, the cochlea is traversed by a conical column, the *modiolus*, around which a *spiral canal* winds with

Fig. 297.*

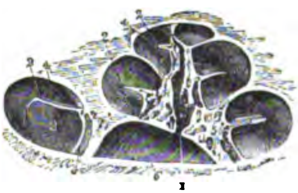
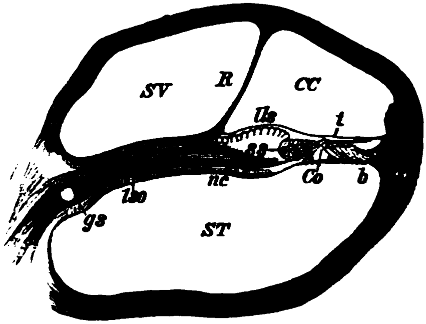


Fig. 298.†



* Fig. 297. View of the osseous cochlea divided through the middle (Arnold). ‡.—1, central canal of the modiolus ; 2, lamina spiralis ossea ; 3, scala tympani ; 4, scala vestibuli ; 5, porous substance of the modiolus near one of the sections of the canalis spiralis modioli.

† Fig. 298. Altered from Henle. Section through one of the coils of the cochlea (diagrammatic), (from *Quain's Anatomy*). *S T*, scala tympani ; *S V*, scala vestibuli ; *C C*, canalis cochleæ or canalis membranaceus ; *R*, membrane of Reissner ; *l s o*, lamina spiralis ossea ; *l l s*, limbus laminæ spiralis ; *s s*, sulcus spiralis ; *n c*, cochlear nerve ; *g s*, ganglion spirale ; *t*, membrana tectoria ; (below the membrana tectoria is the lamina reticularis ;) *b*, membrana basilaris ; *Co*, rods of Corti ; *l s p*, ligamentum spirale.

about two turns and a half from the base to the apex. At the apex of the cochlea the canal is closed; at the base it presents three openings, of which one, already mentioned, communicates with the vestibule; another, called *fenestra rotunda*, is separated by a membrane from the cavity of the tympanum; the third is the orifice of the *aquæductus cochleæ*, a canal leading to the jugular fossa of the petrous bone, and corresponding, at least in obscurity of purpose and origin, to the aquæductus vestibuli. The spiral canal is divided into two passages, or scalæ, by a partition of bone and membrane, the *lamina spiralis*. The osseous part or *zone* of this lamina is connected with the modiolus; the membranous part, with a muscular zone, according to Todd and Bowman, forming its outer margin, is attached to the outer wall of the canal. Commencing at the base of the cochlea, between its vestibular and tympanic openings, they form a partition between these apertures; the two scalæ are, therefore, in correspondence with this arrangement, named *scala vestibuli* and *scala tympani* (fig. 298). At the apex of the cochlea, the lamina spiralis ends in a small *hamulus*, the inner and concave part of which, being detached from the summit of the modiolus, leaves a small aperture named *helicotrema*, by which the two scalæ, separated in all the rest of their length, communicate.

Besides the "scala vestibuli" and "scala tympani," there is a third space between them, called the *scala media* or *canalis membranaceus* (CC. fig. 298). In section it is triangular, its external wall being formed by the wall of the cochlea, its upper wall (separating it from the scala vestibuli) by the membrane of Reissner and its lower wall (separating it from the scala tympani), by the basilar membrane, these two meeting at the outer edge of the bony lamina spiralis. Following the turns of the cochlea to its apex, the scala media there terminates blindly; while towards the base of the cochlea it is also closed with the exception of a very narrow passage (canalis reuniens) uniting it with the sacculus. The scala media (like the rest of the membranous labyrinth) contains "endolymph."

Upon the basilar membrane are arranged cells of various shapes.

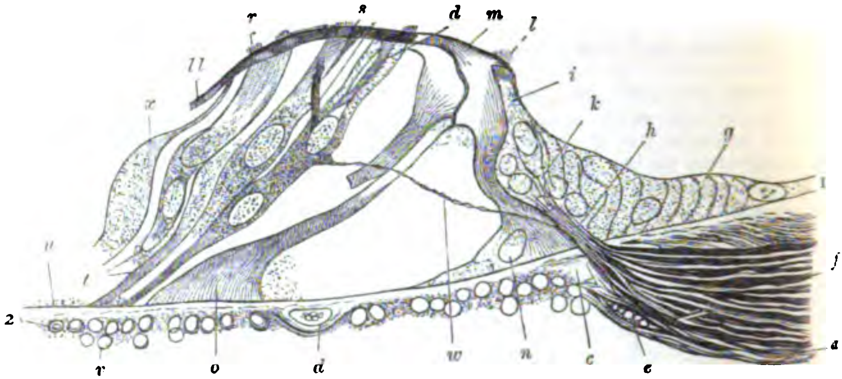
About midway between the outer edge of the lamina spiralis and the outer wall of the cochlea are situated the *rods of Corti*.

Viewed sideways, the rods of Corti are seen to consist of an external and internal pillar, each rising from an expanded foot or *base* on the basilar membrane. They slant inwards towards each other, and each ends in a swelling termed the head; the head of the inner pillar overlying that of the outer (fig. 299). Each pair of pillars forms, as it were, a pointed roof arching over a space, and by a succession of them, a little tunnel is formed.

It has been estimated that there are about 3000 of these pairs of pillars, in proceeding from the base of the cochlea towards its apex. They are found progressively to increase in length, and become more oblique; in other words the tunnel becomes wider, but diminishes in height as we approach the apex of the cochlea. Leaning, as it were, against these external and internal pillars are certain other cells, of which the external ones terminate in small hair-like processes. Most of the above details are shown in the accompanying figure (fig. 299). This complicated structure rests as we have seen upon the basilar membrane; it is roofed in by a remarkable fenestrated membrane (lamina reticularis of Kölliker) into the fenestræ of which the tops of the various rods and cells are received. When viewed from

above, the organ of Corti shows a remarkable resemblance to the key-board of a piano. In close relation with the rods of Corti and the cells inside and outside them, and probably projecting by free ends into the little "tunnel" containing fluid (roofed in by them), are filaments of the auditory nerve.

Fig. 299.*



The *membranous labyrinth* corresponds generally with the form of the osseous labyrinth, so far as regards the vestibule and semicircular canals, but is separated from the walls of these parts by fluid, except where the nerves enter into connection within it. As already mentioned, the membranous labyrinth contains a fluid called *endolymph;* and between its outer surface and the inner surface of the walls of the vestibule and semicircular canals is another collection of similar fluid, called

* Fig. 299. Vertical section of the organ of Corti from the dog. 1 to 2, homogeneous layer of the so-called membrana basilaris; *u*, vestibular layer; *v*, tympanal layer, with nuclei and protoplasm; *a*, prolongation of tympanal periosteum of lamina spiralis ossea; *c*, thickened commencement of the membrana basilaris near the point of perforation of the nerves *h*; *d*, blood-vessel (vas spirale); *e*, blood-vessel; *f*, nerves; *g*, the epithelium of the sulcus spiralis internus; *i*, internal or tufted cell, with basal process *k*, surrounded with nuclei and protoplasm (of the granular layer), into which the nerve-fibres radiate; *l*, hairs of the internal hair-cell; *n*, base or foot of inner pillar of organ of Corti; *m*, head of the same uniting with the corresponding part of an external pillar, whose under half is missing, while the next pillar beyond, *o*, presents both middle portion and base; *r*, *s*, *d*, three external hair cells; *t*, bases of two neighbouring hair or tufted cells; *x*, so-called supporting cell of Hensen; *w*, nerve-fibre terminating in the first of the external hair-cells; *l l* to *l*, lamina reticularis. × 800 (Waldeyer).

perilymph: so that all the sonorous vibrations impressing the auditory nerves on these parts of the internal ear, are conducted through fluid to a membrane suspended in and containing fluid. In the cochlea, the membranous labyrinth completes the septum between the two *scalæ* and encloses a spiral canal, previously mentioned, called *canalis membranaceus* or *canalis cochleæ* (fig. 298). The fluid in the *scalæ* of the cochlea is continuous with the perilymph in the vestibule and semicircular canals, and there is no fluid external to its lining membrane.

The vestibular portion of the membranous labyrinth comprises two, probably communicating cavities, of which the larger and upper is named the *utriculus;* the lower, the *sacculus.* They are lodged in depressions in the bony labyrinth termed respectively "fovea hemielliptica" and "fovea hemispherica." Into the former open the orifices of the membranous semicircular canals; into the latter the *canalis cochleæ.* The membranous labyrinth of all these parts is laminated, transparent, very vascular, and covered on the inner surface with nucleated cells, of which those that line the ampullæ are prolonged into stiff hair-like processes; the same appearance, but to a much less degree, being visible in the *utricule* and *saccule.* In the cavities of the utriculus and sacculus are small masses of calcareous particles, *otoconia* or *otoliths;* and the same, although in more minute quantities, are to be found in the interior of other parts of the membranous labyrinth.

The *auditory nerve*, for the appropriate exposure of whose filaments to sonorous vibrations all the organs now described are provided, is characterised as a nerve of special sense by its softness (whence it derived its name of *portio mollis* of the seventh pair), and by the fineness of its component fibres. It enters the labyrinth of the ear in two divisions; one for the vestibule and semicircular canals, and the other for the cochlea.

The branches for the vestibule spread out and radiate on the inner surface of the membranous labyrinth: their exact termination is unknown. Those for the semicircular canals pass into the ampullæ, and form, within each of them, a forked projection which corresponds with a septum in the interior of the ampulla. The branches for the cochlea enter it through orifices at the base of the modiolus, which they ascend, and thence successively pass into canals in the osseous part of the lamina spiralis. In the canals of this osseous part or zone, the nerves are arranged in a plexus, containing ganglion cells. Their ultimate termination is not known with certainty; but some of them, without doubt, end in the organ of Corti, probably in cells.

Physiology of Hearing.

All the acoustic contrivances of the organ of hearing are means for conducting the sound, just as the optical apparatus of the eye are media for conducting the light. Since all matter is capable of propagating sonorous vibrations, the simplest conditions must be sufficient for mere hearing; for all substances surrounding the auditory nerve would communicate sound to it. The whole development of the organ of hearing, therefore, can have for its object merely the *rendering more perfect* the propagation of the sonorous vibrations, and their *multiplication* by resonance; and, in fact, all the acoustic apparatus of the organ may be shown to have reference to these two principles.

Functions of the External Ear.

The external auditory passage influences the propagation of sound to the tympanum in three ways:—1, by causing the sonorous undulations, entering directly from the atmosphere, to be transmitted by the air in the passage immediately to the membrana tympani, and thus preventing them from being dispersed; 2, by the walls of the passage conducting the sonorous undulations imparted to the external ear itself, by the shortest path to the attachment of the membrana tympani, and so to this membrane; 3, by the resonance of the column of air contained within the passage; 4, the external ear, especially when the tragus is provided with hairs, is also, doubtless, of service in protecting the meatus and membrana tympani against dust, insects, and the like.

1. As a conductor of undulations of air, the external auditory passage receives the direct undulations of the atmosphere, of which those that enter in the direction of its axis produce the strongest impressions. The undulations which enter the passage obliquely are reflected by its parietes, and thus by reflexion reach the membrana tympani. By reflexion, also, the external meatus receives the undulations which impinge upon the concha of the external ear, when their angle of reflexion is such that they are thrown towards the tragus. Other sonorous undulations, again, which could not enter the meatus from the external air either directly or by reflexion, may still be brought into it by inflexion; undulations, for instance, whose direction is that of the long axis of the head, and which pass over the surface of the ear, must, in accordance with the laws of inflexion, be bent into the

external meatus by its margins. But the action of those undulations which enter the meatus directly, are most intense; and hence we are enabled to judge of the point whence sound comes, by turning one ear in different directions, till it is directed to the point whence the vibrations may pass directly into the meatus, and produce the strongest impressions.

2. The walls of the meatus are also solid conductors of sound; for those vibrations which are communicated to the cartilage of the external ear, and not reflected from it, are propagated by the shortest path through the parietes of the passage to the membrana tympani. Hence, both ears, being close stopped, the sound of a pipe is heard more distinctly when its lower extremity, covered with a membrane, is applied to the cartilage of the external ear itself, than when it is placed in contact with the surface of the head.

3. The external auditory passage is important, inasmuch as the air which it contains, like all insulated masses of air, increases the intensity of sounds by resonance. To convince ourselves of this, we need only lengthen the passage by affixing to it another tube: every sound that is heard, even the sound of our own voice, is then much increased in intensity.

The action of the cartilage of the external ear upon sonorous vibrations is partly to reflect them, and partly to condense and conduct them to the parietes of the external passage. With respect to its reflecting action, the concha is the most important part, since it directs the reflected undulations towards the tragus, whence they are reflected into the auditory passage. The other inequalities of the external ear do not promote hearing by reflexion; and, if the conducting power of the cartilage of the ear were left out of consideration, they might be regarded as destined for no particular use; but receiving the impulses of the air, the cartilage of the external ear, while it reflects a part of them, propagates within itself and condenses the rest, as all other solid and elastic bodies would do.

Regarding the cartilage of the external ear, therefore, as a conductor of sonorous vibrations, all its inequalities, elevations, and depressions, which are useless with regard to reflexion, become of evident importance; for those elevations and depressions upon which the undulations fall perpendicularly, will be affected by them in the most intense degree; and, in consequence of the various form and position of these inequalities, sonorous undulations, in whatever direction they may come, must fall perpendicularly upon the tangent of some one of them. This affords an explanation of the extraordinary form given to this part.

Functions of the Middle Ear: the Tympanum, Ossicula, and Fenestræ.

In animals living in the atmosphere, the sonorous vibrations are conveyed to the auditory nerve by three different media in

succession; namely, the air, the solid parts of the body of the animal and of the auditory apparatus, and the fluid of the labyrinth.

Sonorous vibrations are imparted too imperfectly from air to solid bodies, for the propagation of sound to the internal ear to be adequately effected by that means alone; yet already an instance of its being thus propagated has been mentioned.

In passing from air directly into water, sonorous vibrations suffer also a considerable diminution of their strength; but if a tense membrane exists between the air and the water, the sonorous vibrations are communicated from the former to the latter medium with very great intensity. This fact, of which Müller gives experimental proof, furnishes at once an explanation of the use of the fenestra rotunda, and of the membrane closing it. They are the means of communicating, in full intensity, the vibrations of the air in the tympanum to the fluid of the labyrinth. This peculiar property of membranes is the result, not of their tenuity alone, but of the elasticity and capability of displacement of their particles; and it is not impaired when, like the membrane of the fenestra rotunda, they are not impregnated with moisture.

Sonorous vibrations are also communicated without any perceptible loss of intensity from the air to the water, when to the membrane forming the medium of communication, there is attached a short, solid body, which occupies the greater part of its surface, and is alone in contact with the water. This fact elucidates the action of the fenestra ovalis, and of the plate of the stapes which occupies it, and, with the preceding fact, shows that both fenestræ—that closed by membrane only, and that with which the moveable stapes is connected—transmit very freely the sonorous vibrations from the air to the fluid of the labyrinth.

A small, solid body, fixed in an opening by means of a border of membrane, so as to be moveable, communicates sonorous vibrations from air on the one side, to water, or the fluid of the labyrinth, on the other side, much better than solid media not so constructed. But the propagation of sound to the fluid is ren-

dered much more perfect if the solid conductor thus occupying the opening, or fenestra ovalis, is by its other end fixed to the middle of a tense membrane, which has atmospheric air on both sides.

A tense membrane is a much better conductor of the vibrations of air than any other solid body bounded by definite surfaces: and the vibrations are also communicated very readily by tense membranes to solid bodies in contact with them. Thus, then, the membrana tympani serves for the transmission of sound from the air to the chain of auditory bones. Stretched tightly in its osseous ring, it vibrates with the air in the auditory passage, as any thin tense membrane will, when the air near it is thrown into vibrations by the sounding of a tuning-fork or a musical string. And, from such a tense vibrating membrane, the vibrations are communicated with great intensity to solid bodies which touch it at any point. If, for example, one end of a flat piece of wood be applied to the membrane of a drum, while the other end is held in the hand, vibrations are felt distinctly when the vibrating tuning-fork is held over the membrane without touching it; but the wood alone, isolated from the membrane, will only very feebly propagate the vibrations of the air to the hand.

In comparing the membrana tympani to the membrane of a drum, it is necessary to point out certain important differences.

When a drum is struck, a certain definite tone is elicited (fundamental tone); similarly a drum is thrown into vibration when certain tones are sounded in its neighbourhood, while it is quite unaffected by others. In other words it can only take up and vibrate in response to those tones whose vibrations nearly correspond in number with those of its own fundamental tone. The tympanic membrane can take up an immense range of tones produced by vibrations ranging from 30 to 4000 or 5000 per second. This would be clearly impossible if it were an evenly stretched membrane.

The fact is, that the tympanic membrane is by no means evenly stretched, and this is due partly to its slightly funnel-like form, and partly to its being connected with the chain of auditory ossicles. Further, if the membrane were quite free in its centre, it would go on vibrating as a drum does some time after it is struck, and each sound would be prolonged, leading to considerable confusion. This evil is obviated by the ear-bones, which check the continuance of the vibrations like the "dampers" in a pianoforte.

The ossicula of the ear are the better conductors of the sonorous vibrations communicated to them, on account of being

isolated by an atmosphere of air, and not continuous with the bones of the cranium; for every solid body thus isolated by a different medium, propagates vibrations with more intensity through its own substance than it communicates them to the surrounding medium, which thus prevents a dispersion of the sound; just as the vibrations of the air in the tubes used for conducting the voice from one apartment to another are prevented from being dispersed by the solid walls of the tube. The vibrations of the membrana tympani are transmitted, therefore, by the chain of ossicula to the fenestra ovalis and fluid of the labyrinth, their dispersion in the tympanum being prevented by the difficulty of the transition of vibrations from solid to gaseous bodies.

The necessity of the presence of air on the inner side of the membrana tympani, in order to enable it and the ossicula auditus to fulfil the objects just described, is obvious. Without this provision, neither would the vibrations of the membrane be free, nor the chain of bones isolated, so as to propagate the sonorous undulations with concentration of their intensity. But while the oscillations of the membrana tympani are readily communicated to the air in the cavity of the tympanum, those of the solid ossicula will not be conducted away by the air, but will be propagated to the labyrinth without being dispersed in the tympanum.

The propagation of sound through the ossicula of the tympanum to the labyrinth, must be effected either by oscillations of the bones, or by a kind of molecular vibration of their particles, or, most probably, by both these kinds of motion.

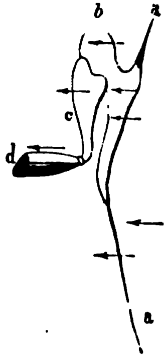
Edouard Weber has shown that the existence of the membrane over the fenestra rotunda will permit approximation and removal of the stapes to and from the labyrinth. When by the stapes the membrane of the fenestra ovalis is pressed towards the labyrinth, the membrane of the fenestra rotunda may, by the pressure communicated through the fluid of the labyrinth, be pressed towards the cavity of the tympanum.

The long process of the malleus receives the undulations of the membrana tympani (fig. 300, *a*, *a*) and of the air in a direction indicated by the arrows, nearly perpendicular to itself. From the long process of the malleus they are propagated to its head (*b*); thence into the incus (*c*), the long process of which is parallel with the long process of the malleus. From the long

process of the incus the undulations are communicated to the stapes (*d*), which is united to the incus at right angles. The several changes in the direction of the chain of bones have, however, no influence on that of the undulations, which remains the same as it was in the meatus externus and long process of the malleus, so that the undulations are communicated by the stapes to the fenestra ovalis in a perpendicular direction.

Increasing tension of the membrana tympani diminishes the facility of transmission of sonorous undulations from the air to it.

Fig. 300.



Mr. Savart observed that the dry membrana tympani, on the approach of a body emitting a loud sound, rejected particles of sand strewn upon it more strongly when lax than when very tense; and inferred, therefore, that hearing is rendered less acute by increasing the tension of the membrana tympani. Müller has confirmed this by experiments with small membranes arranged so as to imitate the membrana tympani; and it may be confirmed also by observations on one's self.

The pharyngeal orifice of the Eustachian tube is usually shut; during swallowing, however, it is opened: this may be shown as follows. If the nose and mouth be closed and the cheeks blown out, a sense of pressure is produced in both ears the moment we swallow; this is due, doubtless, to the bulging out of the tympanic membrane by the compressed air which, at that moment, enters the Eustachian tube.

Similarly the tympanic membrane may be pressed in by rarefying the air in the tympanum. This can be readily accomplished by closing the mouth and nose, and making an inspiratory effort and at the same time swallowing (Valsalva). In both cases the sense of hearing is temporarily dulled; proving that equality of pressure on both sides of the tympanic membrane is necessary for its full efficiency.

The principal office of the Eustachian tube, in Müller's opinion, has relation to the prevention of these effects of increased tension of the membrana tympani. Its existence and openness will provide for the maintenance of the equilibrium between the air within the tympanum and the external air, so as to prevent the inordinate tension of the membrana tympani which would be produced by too great or too little pressure on either side. While discharging this office, however, it will serve to render sounds clearer, as (Henle suggests) the apertures in violins do; to

supply the tympanum with air; and to be an outlet for mucus. If the Eustachian tube were *permanently* open, the sound of one's own voice would probably be greatly intensified, a condition which would of course interfere with the perception of other sounds. At any rate, it is certain that sonorous vibrations can be propagated up the Eustachian tube to the tympanum by means of a tube inserted into the pharyngeal orifice of the Eustachian tube.

The influence of the tensor tympani muscle in modifying hearing may also be probably explained in connection with the regulation of the tension of the membrana tympani. If, through reflex nervous action, it can be excited to contraction by a very loud sound, just as the iris and orbicularis palpebrarum muscle are by a very intense light, then it is manifest that a very intense sound would, through the action of this muscle, induce a deafening or muffling of the ears. In favour of this supposition we have the fact that a loud sound excites, by reflection, nervous action, winking of the eyelids, and, in persons of irritable nervous system, a sudden contraction of many muscles.

The influence of the stapedius muscle in hearing is unknown. It acts upon the stapes in such a manner as to make it rest obliquely in the fenestra ovalis, depressing that side of it on which it acts, and elevating the other side to the same extent.

When the fenestra ovalis and fenestra rotunda exist together with a tympanum, the sound is transmitted to the fluid of the internal ear in two ways,—namely, by solid bodies and by membrane; by both of which conducting media sonorous vibrations are communicated to water with considerable intensity. The sound being conducted to the labyrinth by two paths, will of course produce so much the stronger impression; for undulations will be thus excited in the fluid of the labyrinth from two different though contiguous points; and by the crossing of these undulations stationary waves of increased intensity will be produced in the fluid. Müller's experiments show that the same vibrations of the air act upon the fluid of the labyrinth with much greater intensity through the medium of the chain of auditory bones and the fenestra ovalis than through the medium of the air of the tympanum and the membrane closing the fenestra rotunda: but the cases of disease in which the ossicula have been lost without loss of hearing, prove that sound may also be well conducted through the air of the tympanum and the membrane of the fenestra rotunda.

Functions of the Labyrinth.

The fluid of the labyrinth is the most general and constant of the acoustic provisions of the labyrinth. In all forms of organs of hearing, the sonorous vibrations affect the auditory nerve through the medium of liquid—the most convenient medium, on many accounts, for such a purpose.

The function usually ascribed to the *semicircular canals* is the collecting in their fluid contents, the sonorous undulations from the bones of the cranium. They have probably, also, in some degree, the power of conducting sounds in the direction of their curved cavities more easily than the sounds are carried off by the surrounding hard parts in the original direction of the undulations, though this conducting power is in them much less perfect than in tubes containing air.

Admitting that they have these powers, the increased intensity of the sonorous vibrations thus attained will be of advantage in acting on the auditory nerve where it is expanded in the ampullæ of the canals, and in the utriculus. Where the membranous canals are in contact with the solid parietes of the tubes, this action must be much more intense. But the membranous semicircular canals must have a function independent of the surrounding hard parts; for in the Petromyzon they are not separately enclosed in solid substance, but lie in one common cavity with the utriculus.

The *crystalline pulverulent masses* (otoliths) in the labyrinth would reinforce the sonorous vibrations by their resonance, even if they did not actually touch the membranes upon which the nerves are expanded; but, inasmuch as these bodies lie in contact with the membranous parts of the labyrinth, and the vestibular nerve-fibres are imbedded in them, they communicate to these membranes and the nerves, vibratory impulses of greater intensity than the fluid of the labyrinth can impart. This appears to be their office. Sonorous undulations in water are not perceived by the hand itself immersed in the water, but are felt distinctly through the medium of a rod held in the hand.

The fine hair-like prolongations from the epithelial cells of the ampullæ have, probably, the same function.

The *cochlea* seems to be constructed for the spreading out of he nerve-fibres over a wide extent of surface, upon a solid lamina which communicates with the solid walls of the labyrinth and cranium, at the same time that it is in contact with the fluid of the labyrinth, and which, besides exposing the nerve-fibres to the influence of sonorous undulations by two media, is itself insulated by fluid on either side.

The connection of the lamina spiralis with the solid walls of the labyrinth, adapts the cochlea for the perception of the sonorous undulations propagated by the solid parts of the head and the walls of the labyrinth. The membranous labyrinth of the vestibule and semicircular canals is suspended free in the perilymph, and is destined more particularly for the perception of sounds through the medium of that fluid, whether the sonorous undulations be imparted to the fluid through the fenestræ, or by the intervention of the cranial bones, as when sounding bodies are brought into communication with the head or teeth. The spiral lamina on which the nervous fibres are expanded in the cochlea, is, on the contrary, continuous with the solid walls of the labyrinth, and receives directly from them the impulses which they transmit. This is an important advantage; for the impulses imparted by solid bodies, have, *cæteris paribus*, a greater absolute intensity than those communicated by water. And, even when a sound is excited in the water, the sonorous undulations are more intense in the water near the surface of the vessel containing it, than in other parts of the water equally distant from the point of origin of the sound: thus we may conclude that, *cæteris paribus*, the sonorous undulations of solid bodies act with greater intensity than those of water. Hence we perceive at once an important use of the cochlea.

This is not, however, the sole office of the cochlea; the spiral lamina, as well as the membranous labyrinth, receives sonorous impulses through the medium of the fluid of the labyrinth from the cavity of the vestibule, and from the fenestra rotunda. The lamina spiralis is, indeed, much better calculated to render the

action of these undulations upon the auditory nerve efficient, than the membranous labyrinth is; for, as a solid body insulated by a different medium, it is capable of resonance.

The *rods of Corti* are probably arranged so that each is set to vibrate in unison with a particular tone, and thus strike a particular note, the sensation of which is carried to the brain by those filaments of the auditory nerve with which the little vibrating rod is connected. The distinctive function, therefore, of these minute bodies is, probably, to render sensible to the brain the various musical notes and tones, one of them answering to one tone, and one to another; while perhaps the other parts of the organ of hearing discriminate between the intensities of different sounds, rather than their qualities.

"In the cochlea we have to do with a series of apparatus adapted for performing sympathetic vibrations with wonderful exactness. We have here before us a musical instrument which is designed, not to create musical sounds, but to render them perceptible, and which is similar in construction to artifical musical instruments, but which far surpasses them in the delicacy as well as the simplicity of its execution. For, while in a piano every string must have a separate hammer by means of which it is sounded, the ear possesses a single hammer of an ingenious form in its ear-bones, which can make every string of the organ of Corti sound separately." (Bernstein.)

About 3000 rods of Corti are present in the human ear; this would give about 400 to each of the seven octaves which are within the compass of the ear. Thus about 32 would go to each semi-*tone*. Weber asserts that accomplished musicians can appreciate differences in pitch as small as $\frac{1}{64}$th of a tone. Thus on the theory above advanced, the delicacy of discrimination would, in this case, appear to have reached its limits.

Sensibility of the Auditory Nerve.

Any elastic body, *e.g.*, air, a membrane, or a string performing a certain number of regular vibrations in the second, gives rise to what is termed a musical sound or *tone*. We must, however, distinguish between a musical sound and a mere noise; the latter being due to irregular vibrations.

Musical sounds are distinguished from each other by three qualities. 1. *Strength* or intensity, which is due to the amplitude or length of the vibrations. 2. *Pitch*, which depends upon the number of vibrations in a second. 3. *Quality, Colour*, or *Timbre*. It is by this property that we distinguish the same note sounded on two instruments, *e.g.*, a piano and a flute. It has been proved by Helmholtz to depend on the number of secondary notes, termed *harmonics*, which are present with the predominating or fundamental tone.

It would appear that two impulses, which are equivalent to four single or half vibrations, are sufficient to produce a definite note, audible as such through the auditory nerve. The note produced by the shocks of the teeth of a revolving wheel, at regular intervals upon a solid body, is still heard when the teeth of the wheel are removed in succession, until two only are left; the sound produced by the impulse of these two teeth has still the same definite value in the scale of music.

The maximum and minimum of the intervals of successive impulses still appreciable through the auditory nerve as determinate sounds, have been determined by M. Savart. If their intensity is sufficiently great, sounds are still audible which result from the succession of 48,000 half vibrations, or 24,000 impulses in a second; and this, probably, is not the extreme limit in acuteness of sounds perceptible by the ear. For the opposite extreme, he has succeeded in rendering sounds audible which were produced by only fourteen or eighteen half vibrations, or seven or eight impulses in a second; and sounds still deeper might probably be heard, if the individual impulses could be sufficiently prolonged.

By removing one or several teeth from the toothed wheel before mentioned, M. Savart was enabled to satisfy himself of the fact that in the case of the auditory nerve, as in that of the optic nerve, the sensation continues longer than the impression which causes it; for the removal of a tooth from the wheel produced no interruption of the sound. The gradual cessation of the sensation of sound renders it difficult, however, to determine its exact duration beyond that of the impression of the sonorous impulses.

The power of perceiving the *direction of sounds* is not a faculty of the sense of hearing itself, but is an act of the mind judging on experience previously acquired. From the modifications which the sensation of sound undergoes according to the direction in which the sound reaches us, the mind infers the position of the sounding body. The only true guide for this inference is

the more intense action of the sound upon one than upon the other ear. But even here there is room for much deception, by the influence of reflexion or resonance, and by the propagation of sound from a distance, without loss of intensity, through curved conducting-tubes filled with air. By means of such tubes, or of solid conductors, which convey the sonorous vibrations from their source to a distant resonant body, sounds may be made to appear to originate in a new situation.

The direction of sound may also be judged of by means of one ear only; the position of the ear and head being varied, so that the sonorous undulations at one moment fall upon the ear in a perpendicular direction, at another moment obliquely. But when neither of these circumstances can guide us in distinguishing the direction of sound, as when it falls equally upon both ears, its source being, for example, either directly in front or behind us, it becomes impossible to determine whence the sound comes.

The *distance of the source of sounds* is not recognised by the sense itself, but is inferred from their intensity. The sound itself is always seated but in one place, namely, in our ear; but it is interpreted as coming from an exterior soniferous body. When the intensity of the voice is modified in imitation of the effect of distance, it excites the idea of its originating at a distance. Ventriloquists take advantage of the difficulty with which the direction of sound is recognised, and also the influence of the imagination over our judgment, when they direct their voice in a certain direction, and at the same time pretend, themselves, to hear the sounds as coming from thence.

The experiments of Savart, already referred to, prove that the effect of the action of sonorous undulations upon the nerve of hearing, endures somewhat longer than the period during which the undulations are passing through the ear. If, however, the impression of the same sound be very long continued, or constantly repeated for a long time, then the sensation produced may continue for a very long time, more than twelve or twenty-four hours even, after the original cause of the sound has ceased. This must have been experienced by every one who has travelled several days continuously; for some time after the journey, the

rattling noises are heard when the ear is not acted on by other sounds.

We have here a proof that the perception of sound, as sound, is not essentially connected with the existence of undulatory pulses; and that the sensation of sound is a state of the auditory nerve, which, though it may be excited by a succession of impulses, may also be produced by other causes. Even if it be supposed that undulations excited by the impulse are kept up in the auditory nerve for a certain time, they must be undulations of the nervous principle itself, which, being excited, continue until the equilibrium is restored.

Corresponding to the double vision of the same object with the two eyes, is the double hearing with the two ears; and analogous to the double vision with one eye, dependent on unequal refraction, is the double hearing of a single sound with one ear, owing to the sound coming to the ear through media of unequal conducting power. The first kind of double hearing is very rare; instances of it are recorded, however, by Sauvages and Itard. The second kind, which depends on the unequal conducting power of two media through which the same sound is transmitted to the ear, may easily be experienced. If a small bell be sounded in water, while the ears are closed by plugs, and a solid conductor be interposed between the water and the ear, two sounds will be heard differing in intensity and tone; one being conveyed to the ear through the medium of the atmosphere, the other through the conducting-rod.

The sense of vision may vary in its degree of perfection as regards either the faculty of adjustment to different distances, the power of distinguishing accurately the particles of the retina affected, sensibility to light and darkness, or the perception of the different shades of colour. In the sense of hearing, there is no parallel to the faculty by which the eye is accommodated to distance, nor to the perception of the particular part of the nerve affected; but just as one person sees distinctly only in a bright light, and another only in a moderate light, so in different individuals the sense of hearing is more perfect for sounds of different pitch; and just as a person whose vision for the forms of objects,

etc., is acute, nevertheless distinguishes colours with difficulty, and has no perception of the harmony and disharmony of colours, so one, whose hearing is good as far as regards the sensibility to feeble sounds, is sometimes deficient in the power of recognising the musical relation of sounds, and in the sense of harmony and discord; while another individual, whose hearing is in other respects imperfect, has these endowments. The causes of these differences are unknown.

Subjective sounds are the result of a state of irritation or excitement of the auditory nerve produced by other causes than sonorous impulses. A state of excitement of this nerve, however induced, gives rise to the sensation of sound. Hence the ringing and buzzing in the ears heard by persons of irritable and exhausted nervous system, and by patients with cerebral disease, or disease of the auditory nerve itself; hence also the noise in the ears heard for some time after a long journey in a rattling noisy vehicle. Ritter found that electricity also excites a sound in the ears.

From the above truly subjective sound we must distinguish those dependent, not on a state of the auditory nerve itself merely, but on sonorous vibrations excited in the auditory apparatus. Such are the buzzing sounds attendant on vascular congestion of the head and ear, or on aneurismal dilatation of the vessels. Frequently even the simple pulsatory circulation of the blood in the ear is heard. To the sounds of this class belong also the buzz or hum heard during the contraction of the palatine muscles in the act of yawning; during the forcing of air into the tympanum, so as make tense the membrana tympani; and in the act of blowing the nose, as well as during the forcible depression of the lower jaw.

Irritation or excitement of the auditory nerve is capable of giving rise to movements in the body, and to sensations in other organs of sense. In both cases it is probable that the laws of reflex action, through the medium of the brain, come into play. An intense and sudden noise excites, in every person, closure of the eyelids, and, in nervous individuals, a start of the whole body or an unpleasant sensation, like that produced by an electric

shock, throughout the body, and sometimes a particular feeling in the external ear. Various sounds cause in many people a disagreeable feeling in the teeth, or a sensation of cold tickling through the body, and, in some people, intense sounds are said to make the saliva collect.

The sense of hearing may in its turn be affected by impressions on many other parts of the body; especially in diseases of the abdominal viscera, and in febrile affections. Here, also, it is probable that the central organs of the nervous system are the media through which the impression is transmitted.

THE SENSE OF SIGHT.

Eyelids and Lachrymal Apparatus.

The *eyelids* consist of two moveable folds of skin, each of which is kept in shape by a thin plate of cartilage (*tarsal cartilage*). Along their free edges are inserted a number of curved hairs (*eyelashes*), which, when the lids are half closed, serve to protect the eye from dust and other foreign bodies: their tactile sensibility is also very delicate.

On the inner surface of the tarsal cartilages are disposed a number of small racemose glands (Meibomian), whose ducts open near the free edge of the lid.

The orbital surface of each lid is lined by a delicate, highly sensitive mucous membrane (*conjunctiva*), which is continuous with the skin at the free edge of each lid, and after lining the inner surface of the eyelid is reflected on to the eyeball, being somewhat loosely adherent to the sclerotic coat. The epithelial layer is continued over the cornea as its anterior epithelium. At the inner edge of the eye the conjunctiva becomes continuous with the mucous lining of the lachrymal sac and duct, which again is continuous with the mucous membrane of the inferior meatus of the nose.

The *lachrymal gland* is lodged in the upper and outer angle of the orbit. Its secretion, which issues from several ducts on the inner surface of the upper lid, under ordinary circumstances just suffices to keep the conjunctiva moist. It passes out through

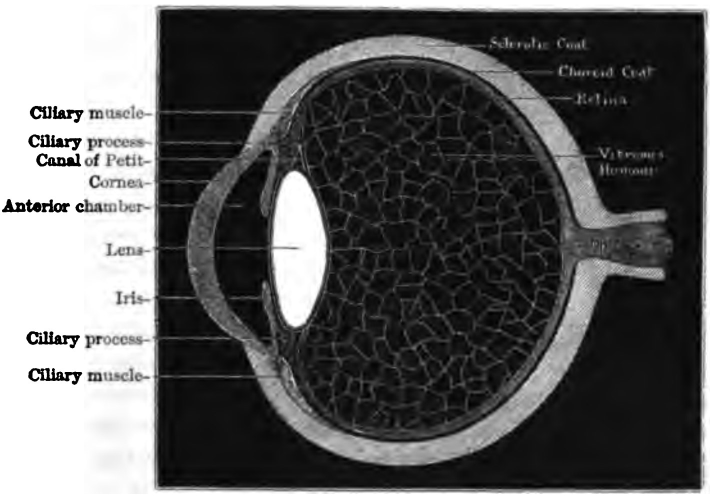
two small openings (puncta lachrymalia) near the inner angle of the eye, one in each lid, into the lachrymal sac, and thence along the nasal duct into the inferior meatus of the nose. The excessive secretion poured out under the influence of any irritating vapour or painful emotion overflows the lower lid in the form of tears.

The eyelids are closed by the contraction of a sphincter muscle (*orbicularis*), supplied by the Facial nerve; the upper lid is raised by the *Levator palpebræ superioris*, which is supplied by the Third nerve.

THE EYEBALL.

The eyeball or the organ of vision (fig. 301) consists of a variety of structures which may be thus enumerated :—

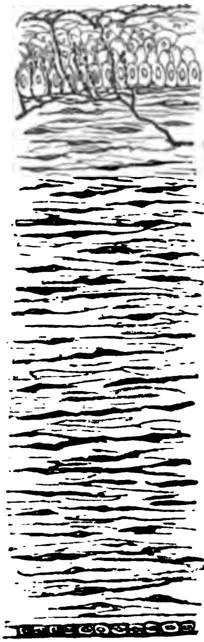
Fig. 301.



The *sclerotic*, or outermost coat, envelopes about five-sixths of the eyeball: continuous with it, in front, and occupying the remaining sixth, is the *cornea*. Immediately within the sclerotic is the *choroid* coat, and within the choroid is the *retina*. The interior of the eyeball is well-nigh filled by the *aqueous* and *vitreous humours* and the *crystalline lens*; but also, there is

suspended in the interior a contractile and perforated curtain,—the *iris*, for regulating the admission of light, and behind the junction of the sclerotic and cornea is the ciliary muscle, the function of which is to adapt the eye for seeing objects at various distances.

Fig. 302.*



These structures may be examined rather more in detail.

The *sclerotic* coat is composed of connective tissue, arranged in variously disposed and intercommunicating layers. It is strong, tough, and opaque, and not very elastic.

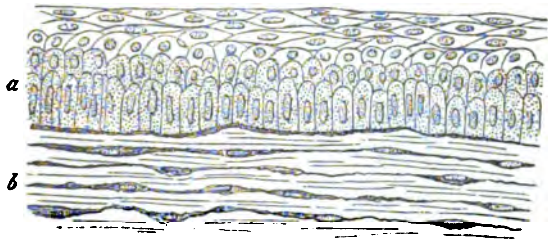
The *cornea* is a transparent membrane which forms a segment of a smaller sphere than the rest of the eyeball, and is let in, as it were, into the sclerotic with which it is continuous all round. It is coated with a laminated anterior epithelium (*a*, fig. 303) consisting of seven or eight layers of cells, of which the superficial ones are flattened and scaly, and the deeper ones more or less columnar. Immediately beneath this is the anterior elastic lamina (Bowman).

The cornea tissue proper as well as its epithelium is, in the adult, completely destitute of blood-vessels; it consists of an intercellular ground-substance of rather obscurely fibrillated flattened bundles of connective tissue, arranged parallel to the free surface, and forming the boundaries of branched anasto-

* Fig. 302. Vertical section of Rabbit's cornea, stained with chloride of gold. *e*. Laminated anterior epithelium. Immediately beneath this is the anterior elastic lamina of Bowman. *n*. Nerves forming a delicate sub-epithelial plexus, and sending up fine twigs between the epithelial cells to end in a second plexus on the free surface. *d*. Descemet's membrane, consisting of a fine elastic layer, and a single layer of epithelial cells. The substance of the cornea *f*, is seen to be fibrillated, and contains many layers of branched corpuscles, arranged parallel to the free surface, and here seen edgewise (Schofield).

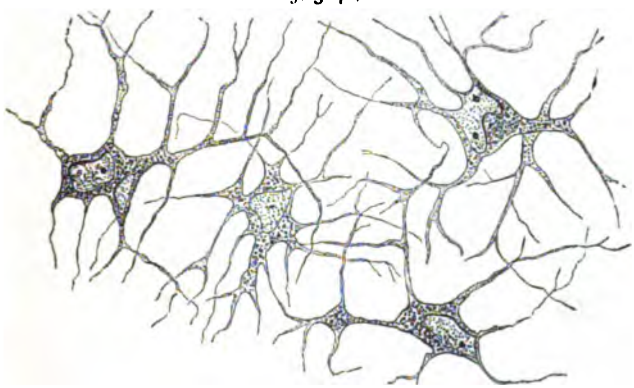
mosing spaces in which the cornea-corpuscles lie. These branched cornea-corpuscles have been seen to creep by amœboid

Fig. 303.*



movement from one branched space into another. At its posterior surface the cornea is limited by the posterior elastic

Fig. 304.†



lamina, or membrane of Descemet, the inner layer of which consists of a single stratum of epithelial cells (fig. 302, *d.*).

The nerves of the cornea are both large and numerous: they are derived from the ciliary nerves. They traverse the substance of the cornea, in which some of them terminate, in the direction of its anterior surface, near which the axis cylinders break up into bundles of very delicate beaded

* Fig. 303. Vertical section of Rabbit's cornea. *a.* Anterior epithelium, showing the different shapes of the cells at various depths from the free surface. *b.* Portion of the substance of cornea (Klein).

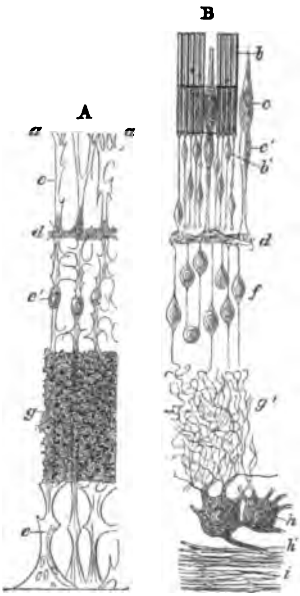
† Fig. 304. Horizontal preparation of cornea of frog; showing the network of branched cornea corpuscles. The ground-substance is completely colourless. × 400. (Klein.)

fibrillæ (fig. 302): these form a plexus immediately beneath the epithelium, from which delicate fibrils pass up between the epithelial cells to the free surface, where they terminate either singly or by forming a second plexus.

The *choroid* (*tunica vasculosa*) is lined internally by a single layer of tessellated pigmented epithelium (fig. 12) which, (see Chapter on Development) strictly speaking, forms part of the Retina. External to this is a very rich network of capillaries (chorio-capillaris), outside which again are connective-tissue layers of stellate pigmented cells (fig. 24.) with numerous arteries and veins.

The principal use of the choroid is to absorb, by means of its pigment, those rays of light which pass through the transparent retina, and thus to prevent their being thrown again upon the retina, so as to interfere with the distinctness of the images there formed. Hence animals in which the choroid is destitute of pigment, and human Albinoes, are dazzled by daylight and see best in the twilight. The choroid coat ends in front in what are called the *ciliary processes* (fig. 306).

Fig. 305.*



The *retina* (fig. 307) is a delicate membrane, concave, with the concavity directed forwards and ending in front, near the outer part of the ciliary processes in a finely notched edge,—the *ora serrata*. Semi-transparent when fresh, it soon becomes clouded and

* Fig. 305. Diagram of the retina (Max Schultze). A. connective tissue portion. B. Nervous portion. *The two must be combined to form the complete retina.* *aa.* Membrana limitans externa. *b.* Rods. *c.* Cones. *b'.* Rod-granule. *c'.* Cone-granule; both belonging to the external granule layer. *e.* Müller's sustentacular fibres, with their nuclei *e'*. *d.* Intergranular layer. *f.* Internal granule-layer. *g.* Molecular layer, connective-tissue portion. *g'.* Molecular layer, nerve-fibril portion. *h.* Ganglion cells. *h'.* Their axis-cylinder process. *i.* Nerve-fibre layer.

opaque, with a pinkish tint from the blood in its minute vessels. It results from the sudden spreading out or expansion of the optic nerve, of whose terminal fibres, apparently deprived of their external white substance, together with nerve-cells, it is essentially composed.

Fig. 306.*

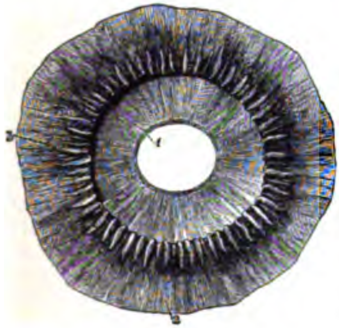
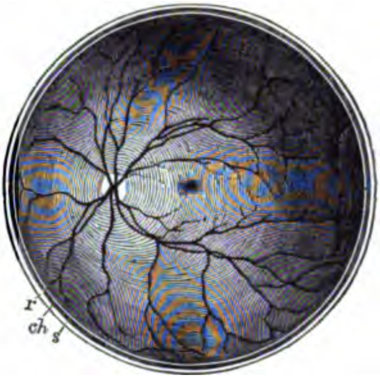


Fig. 307.†



Exactly in the centre of the retina, and at a point thus corresponding to the axis of the eye in which the sense of vision is most perfect, is a round yellowish elevated spot, about $\frac{1}{24}$ of an inch in diameter, having a minute aperture at its summit, and called after its discoverer the *yellow spot of Sœmmering.* In its centre is a minute depression called *fovea centralis.* About $\frac{1}{10}$ of an inch to the inner side of the yellow spot, and consequently of the axis of the eye, is the point at which the optic nerve spreads

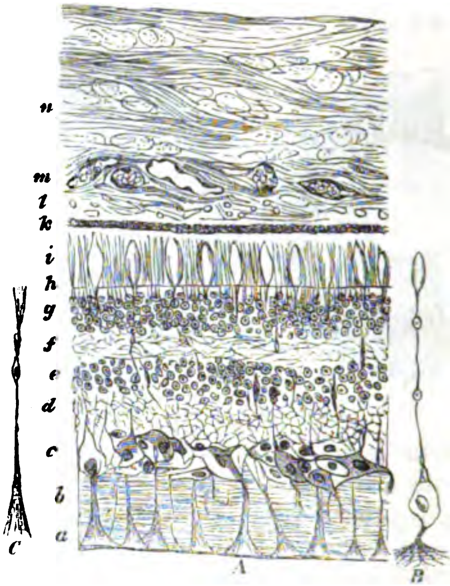
* Fig. 306. Ciliary processes as seen from behind. ½.—1, posterior surface of the iris, with the sphincter muscle of the pupil; 2, anterior part of the choroid coat; 3, one of the ciliary processes, of which about seventy are represented.

† Fig. 307. The posterior half of the retina of the left eye viewed from before (after Henle); *s*, the cut edge of the sclerotic coat; *ch*, the choroid; *r*, the retina; in the interior at the middle, the macula lutea with the depression of the fovea centralis is represented by a slight oval shade; towards the left side the light spot indicates the colliculus or eminence at the entrance of the optic nerve, from the centre of which the arteria centralis is seen spreading its branches into the retina, leaving the part occupied by the macula comparatively free.

out its fibres to form the retina. This is the only point of the surface of the retina from which the power of vision is absent.

The retina consists of certain nervous elements arranged in several layers, and supported by a very delicate connective tissue.

Fig. 308.*



From the nature of the case there is still considerable uncertainty as to the character (nervous or connective tissue) of some of the layers of the retina. The following nine layers, from within outwards, are usually to be distinguished in a vertical section (figs. 305, 308).

* Fig. 308. A. Section of the retina, choroid, and part of the sclerotic, moderately magnified. (*a.*) Membrana limitans interna. (*b.*) Nerve-fibre layer traversed by Müller's sustentacular fibres (of the connective tissue system). (*c.*) Ganglion-cell layer. (*d.*) Molecular layer. (*e.*) Internal granule layer. (*f.*) Intergranular layer. (*g.*) External granule layer. (*h.*) Membrana limitans interna, running along the lower part of (*i*) the layer of rods and cones. The cones in the woodcut are not sufficiently regular. (*k.*) Pigment cell layer of the choroid in which the ends of the rods and cones should be imbedded, but from which they have been slightly torn away in cutting the section. (*l*, *m.*) Internal and external vascular portions of the choroid, the first containing capillaries, the second larger blood-vessels, cut in transverse section. (*n.*) Sclerotic. B, C. Diagrams of the nerve tissue, and connective tissue elements of the retina respectively (imitated from Max Schultze) (W. Pye).

1. *Membrana limitans interna:* a delicate membrane in contact with the vitreous humour.

2. *Fibres of optic nerve.* This layer is of very varying thickness in different parts of the retina: it consists chiefly of non-medullated fibres which interlace, and some of which are continuous with processes of the large nerve-cells forming the next layer.

3. *Layer of ganglionic corpuscles*, consisting of large multipolar nerve-cells, sometimes forming a single layer. In some parts of the retina, especially near the *macula lutea*, this layer is very thick, consisting of several distinct strata of nerve-cells. These cells lie in the spaces of a connective-tissue framework.

4. *Molecular layer.* This presents a finely granulated appearance. It consists of a punctiform connective tissue traversed by numberless very fine fibrillar processes of the nerve-cells.

5. *Internal granular layer.* This consists chiefly of numerous small round cells with a very small quantity of protoplasm surrounding a large nucleus; they are generally bipolar, giving off one process outwards and another inwards. They greatly resemble the ganglionic corpuscles of the cerebellum (fig. 241). Besides these there are large oval nuclei (*d'*, fig. 305, A) belonging to the sustentacular connective tissue fibres.

6. *Intergranular layer;* which closely resembles the molecular layer but is much thinner. It consists of finely-dotted connective tissue with nerve-fibrils.

7. *External granular layer;* which consists of several strata of small cells resembling those of the internal granular layer; they have been classed as rod and cone granules, according as they are connected by very delicate fibrils with the rods and cones respectively. They are lodged in the meshes of a connective tissue framework. Both the internal and external granular layer stain very rapidly and deeply with hæmatoxylin, while the rod and cone layer remains quite unstained.

8. *Membrana limitans externa;* a delicate, well-defined membrane, clearly marking the internal limit of the rod and cone layer.

9. *Rod and cone layer, bacillar layer, or membrane of Jacob*, consisting of two kinds of elements: the "rods," which are cylindrical and of uniform diameter throughout, and the "cones," whose internal portion is distinctly conical, and surmounted externally by a thin rod-like body. According to the researches of Max Schultze, the rods show traces of longitudinal fibrillation, and, moreover, have a great tendency to break up into a number of transverse discs like a pile of coins.

In the rod and cone layer of birds, the cones usually predominate largely in number, whereas in man the rods are by far the more numerous. In nocturnal birds, however, such as the owl, only rods are present, and the same appears to be the case in many nocturnal and burrowing mammalia, *e.g.*, bat, hedge-hog, mouse, and mole.

In the centre of the yellow spot (macula lutea), all the layers of the retina become greatly thinned out and almost disappear, except the rod and cone layer, which considerably increases in thickness, and comes to consist almost entirely of long slender

cones, the rods being very few in number, or entirely absent. There are capillaries here, but none of the larger branches of the retinal arteries.

With regard to the connection of the various layers there is still some uncertainty. Fig. 305 represents the view of Max Schultze. According to this there are certain sustentacular fibres of connective tissue (radiating fibres of Müller) which spring from the *membrana limitans interna* almost vertically, and traverse the retina to the *limitans externa*, whence very delicate connective tissue processes pass up between the rods and cones. The framework which they form is represented in fig. 305, A. The *nervous* elements of the retina are represented in fig. 305, B, and consist of delicate fibres passing up from the nerve-fibre layer to the rods and cones, and connected with the ganglionic corpuscles and granules of the internal and external layer.

The eye is very richly supplied with blood-vessels. In addition to the conjunctival vessels which are derived from the palpebral and lachrymal arteries, there are at least two other distinct sets of vessels supplying the tunics of the eyeball. (1.) The vessels of the sclerotic, choroid, and iris, and (2.) The vessels of the retina.

(1). These are the short and long *posterior* ciliary arteries which pierce the sclerotic in the posterior half of the eyeball, and the *anterior* ciliary which enter near the insertions of the recti. These vessels anastomose and form a very rich choroidal plexus; they also supply the iris and ciliary processes, forming a very highly vascular circle round the outer margin of the iris and adjoining portion of the sclerotic.

The distinctness of these vessels from those of the conjunctiva is well seen in the difference between the bright red of blood-shot eyes (conjunctival congestion), and the pink zone surrounding the cornea which indicates deep seated ciliary congestion.

(2). The *retinal vessels* (fig. 307) are derived from the *arteria centralis retinæ*, which enters the eyeball along the centre of the optic nerve. They ramify all over the retina, chiefly in its inner layers. They can be seen by direct ophthalmoscopic examination (p. 693) and also indirectly as follows:—

If a small lighted candle be moved to and fro at the side of and close to one eye in a dark room while the eyes look steadily forward into the darkness, a remarkable branching figure (Purkinje's figure) is seen floating before the eye, consisting of dark lines on a reddish ground. As the candle moves the figure moves in the opposite direction, and from its whole appearance there can be no doubt that it is a reversed picture of the retinal vessels projected before the eye. The two large branching arteries passing up and down from the optic disc are clearly visible together with their minutest branches. A little to one side of the disc, in a part free from vessels, is seen the yellow spot in the form of a slight depression.

This remarkable appearance is doubtless due to shadows of the retinal

vessels cast by the candle. Since the light of the candle falls on the retinal vessels from in front, the shadow is cast behind the vessels, and hence those elements of the retina which perceive the shadows must also lie behind the vessels.

Here we have a clear proof that the light-perceiving elements of the retina are not the fibres of the optic nerve forming the innermost layer of the retina, but the external layers of the retina, probably the rods and cones. This is further corroborated by the fact that at that part of the retina in which vision is most acute (*fovea centralis retinæ*) the cones are largest and most numerous, while the other layers are almost absent, and moreover that the "blind spot" contains no rods and cones but only fibres of the optic nerve.

By means of the retina and the other parts just described, a provision is afforded for enabling the terminal fibres of the optic nerve to receive the impression of rays of light, and to communicate them to the brain, in which they excite the sensation of vision. But that light should produce in the retina images of the objects from which it comes, it is necessary that, when emitted or reflected from determinate parts of the external objects, it should stimulate only corresponding parts of the retina. For as light radiates from a luminous body in all directions, when the media offer no impediment to its transmission, a luminous point will necessarily illuminate all parts of a surface, such as the retina opposed to it, and not merely one single point. A retina, therefore, without any optical apparatus placed in front of it to separate the light of different objects, would see nothing distinctly, but would merely perceive the general impression of daylight, and distinguish it from the night. Accordingly, we find that in man, and all vertebrate animals, certain transparent refracting media are placed in front of the retina for the purpose of collecting together into one point, the different divergent rays emitted by each point of the external body, and of giving them such directions that they shall fall on corresponding points of the retina, and thus produce an exact image of the object from which they proceed. These refracting media are, in the order of succession from without inwards, the cornea, the aqueous humour, the crystalline lens, and the vitreous humour (fig. 301).

The *cornea*, the structure of which has been already referred

to (p. 682), is in a twofold manner capable of refracting and causing convergence of the rays of light that fall upon and traverse it. It thus affects them first, by its density; for it is a law in optics that when rays of light pass from a rarer into a denser medium, if they impinge upon the surface in a direction removed from the perpendicular, they are bent out of their former direction towards that of a line perpendicular to the surface of the denser medium; and, secondly, by its convexity; for it is another law in optics that rays of light impinging upon a convex transparent surface, are refracted towards the centre, those being most refracted which are farthest from the centre of the convex surface.

Behind the cornea is a space containing a thin watery fluid, the *aqueous humour*, holding in solution a small quantity of chloride of sodium and extractive matter. The space containing the aqueous humour is divided into an anterior and posterior *chamber* by a membranous partition, *the iris*, to be presently again mentioned. The effect produced by the aqueous humour on the rays of light traversing it, is not yet fully ascertained.

Fig. 309.*

Its chief use, probably, is to assist in filling the eyeball, so as to maintain its proper convexity, and at the same time to furnish a medium in which the movements of the iris can take place.

Behind the aqueous humour and the iris, and imbedded in the anterior part of the medium next to be described, viz., the vitreous humour, is seated a doubly-convex body, the *crystalline lens*, which is the most important refracting structure of the eye. The structure of the lens is very complex. It consists essentially of fibres united side by side to each other, and arranged together in very numerous laminæ, which are so placed upon one another, that when hardened in spirit the lens splits into three portions

* Fig. 309. Laminated structure of the crystalline lens. $\frac{4}{1}$.—The laminæ are split up after hardening in alcohol. 1, the denser central part or nucleus; 2, the successive external layers (Arnold).

in the form of sectors, each of which is composed of superimposed concentric laminæ. The lens increases in density and, consequently, in power of refraction, from without inwards; the central part, usually termed the nucleus, being the most dense. The density of the lens increases with age; it is comparatively soft in infancy, but very firm in advanced life: it is also more spherical at an early period of life than in old age.

The *vitreous humour* constitutes nearly four-fifths of the whole globe of the eye. It fills up the space between the retina and the lens, and its soft jelly-like substance consists essentially of numerous layers, formed of delicate, simple membrane, the spaces between which are filled with a watery, pellucid fluid. It probably exercises some share in refracting the rays of light to the retina; but its principal use appears to be that of giving the proper distension to the globe of the eye, and of keeping the surface of the retina at a proper distance from the lens.

As already observed, the space occupied by the aqueous humour is divided into two portions by a vertically-placed membranous diaphragm, termed the *iris*, provided with a central aperture, the *pupil*, for the transmission of light. The iris is composed of plain muscular fibres imbedded in ordinary fibro-cellular or connective tissue. The muscular fibres of the iris have a direction, for the most part, radiating from the circumference towards the pupil; but as they approach the pupillary margin, they assume a circular direction, and at the very edge form a complete ring. By the contraction of the radiating fibres, the size of the pupil is enlarged: by the contraction of the circular ones, which resemble a kind of sphincter, it is diminished. The object effected by thè movements of the iris, is the regulation of the quantity of light transmitted to the retina; the quantity of which is, *cæteris paribus*, directly proportioned to the size of the pupillary aperture. The posterior surface of the iris is coated with a layer of dark pigment, so that no rays of light can pass to the retina, except such as are admitted through the aperture of the pupil.

This iris is very richly supplied with nerves and blood-vessels. Its circular muscular fibres appear to be supplied by

the third, and its radiating fibres by the fifth cranial nerve and sympathetic.

The close sympathy subsisting between the two eyes is nowhere better shown than by the iris. If one eye be shaded by the hand its pupil will of course dilate; but the pupil of the *other* eye will also dilate, though it is unshaded.

The *ciliary muscle* is composed of plain muscular fibres, which form a narrow zone around the interior of the eye-ball, near the line of junction of the cornea with the sclerotic, and just behind the outer border of the iris (fig. 301). The *outermost* fibres of this muscle are attached in front to the inner part of the sclerotic and cornea at their line of junction, and, diverging somewhat, are fixed to the ciliary processes, and a small portion of the choroid immediately behind them. The *inner* fibres, immediately within the preceding, form a circular zone around the interior of the eye-ball, outside the ciliary processes. They compose the ring formerly called the ciliary ligament.

The function of this muscle is to adapt the eye for seeing objects at various distances. The manner in which it effects this object will be considered afterwards (p. 699).

The contents of the ball of the eye are surrounded and kept in position by the *cornea*, and the dense, fibrous membrane before referred to as the *sclerotic*, which, besides thus encasing the contents of the eye, serves to give attachment to the various muscles by which the movements of the eye-ball are effected. These muscles, and the nerves supplying them, have been already considered (p. 557 *et seq.*).

The Ophthalmoscope.—Every one is perfectly familiar with the fact, that it is quite impossible to see the *fundus* or back of another person's eye by simply looking into it. The interior of the eye forms a perfectly black background to the pupil. The same remark applies to an ordinary photographic camera, and may be illustrated by the difficulty we experience in seeing into a room from the street through the window, unless the room be lighted within. In the case of the eye this fact is partly due to the feebleness of the light reflected from the retina, most of it being absorbed by the choroid, but far more to the fact that every such ray is reflected straight back to the source of light (*e.g.*, candle), and cannot, therefore, be seen by the unaided eye without intercepting the incident light from the candle, as well as the reflected rays from the retina.

This difficulty has been surmounted by the ingenious device of Helmholtz,

now so extensively used, termed the *ophthalmoscope*. As at present used, it consists of a small slightly concave mirror, by which light is reflected from a candle into the eye. The observer looks through a hole in the mirror, and can thus explore the illuminated fundus; the entrance of the optic nerve and the retinal vessels being plainly visible.

Of the Phenomena of Vision.

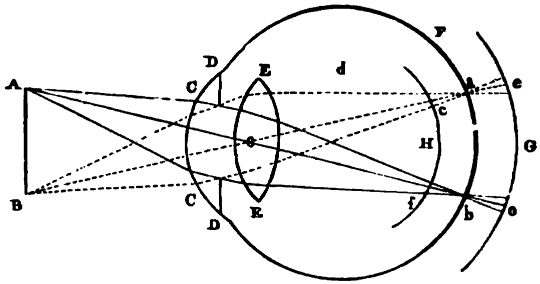
The eye may be compared to the *camera* used by photographers formed by a convex lens. In this instrument images of external objects are thrown upon a ground-glass screen at the back of a box, the interior of which is painted black. In the eye the convex lens is represented by the crystalline lens, the dark box by the eyeball with its choroidal pigment, and the screen by the retina. In the case of the camera the screen is enabled to receive clear images of objects at different distances, by being shifted forward and back: while the convex lens too can be screwed in and out. The corresponding contrivance in the eye, will be described under the head of *Accomodation.*

The essential constituents of the optical apparatus of the eye may be thus enumerated:—(1) a *nervous* structure (retina) to receive and transmit, by way of the optic nerve, to the brain the impressions of light; (2) certain *refracting media* for the purpose of so disposing of the rays of light traversing them as to throw a correct image of an external body on the retina; (3) a contractile diaphragm (*iris*) with a central aperture for regulating the quantity of light admitted into the eye; and (4) a contractile structure (*ciliary muscle*) by which the chief refracting medium shall be so controlled as to enable objects to be seen at various distances; (*accommodation.*)

With the help of the diagram (fig. 310) representing a vertical section of the eye from before backwards, the mode in which, by means of the refracting media of the eye, an image of an object of sight is thrown on the retina, may be rendered intelligible. The rays of the cones of light emitted by the points A B, and every other point of an object placed before the eye, are first refracted, that is, are bent towards the axis of the cone, by the cornea C C, and the aqueous humour contained between it and the lens. The rays of each cone are again refracted and bent still more towards its central ray or axis by the anterior surface of the lens E E; and again as they pass out through its posterior surface into the less dense medium of the vitreous humour. For a lens has the power of refracting and causing the

convergence of the rays of a cone of light, not only on their entrance from a rarer medium into its anterior convex surface, but also at their exit from its posterior convex surface into the rarer medium.

Fig. 310.*



In this manner the rays of the cones of light issuing from the points A and B are again collected to points at *a* and *b*; and, if the retina F be situated at *a* and *b*, perfect, though reversed, images of the points A and B will be formed upon it: but if the retina be not at *a* and *b*, but either before or behind that situation,—for instance, at H or G,—circular luminous spots *c* and *f*, or *e* and *o*, instead of points, will be seen; for at H the rays have not yet met, and at G they have already intersected each other, and are again diverging.

The retina must therefore be situated at the proper focal distance from the lens, otherwise a defined image will not be formed; or, in other words, the rays emitted by a given point of the object will not be collected into a corresponding point of focus upon the retina.

Spherical Aberration.—The rays of a cone of light from an object situated at the side of the field of vision do not meet all in the same point, owing to their unequal refraction; for the refraction of the rays which pass through the circumference of a lens is greater than that of those traversing its central portion. This defect is known as *spherical aberration*, and in the camera, telescope, microscope, and other optical instruments, it is remedied by the interposition of a screen with a circular aperture in the path of the rays of light, cutting off all the marginal rays and only allowing the passage of those near the centre. Such correction is effected in the eye by the iris, which forms an annular diaphragm to cover the circumference of the

lens, and to prevent the rays from passing through any part of the lens but its centre, which corresponds to the pupil. The posterior surface of the iris is coated with pigment, to prevent the passage of rays of light through its substance.

The image of an object will be most defined and distinct when the pupil is narrow, the object at the proper distance for vision, and the light abundant; so that, while a sufficient number of rays are admitted, the narrowness of the pupil may prevent the production of indistinctness of the image by *spherical aberration*. But even the image formed by the rays passing through the circumference of the lens, when the pupil is much dilated, as in the dark, or in a feeble light, may, under certain circumstances, be well defined.

Distinctness of vision, is further secured by the inner surface of the choroid, immediately external to the retina itself, as well as the posterior surface of the iris and the ciliary processes, being coated with black pigment, which absorbs any rays of light that may be reflected within the eye, and prevents their being thrown again upon the retina so as to interfere with the images there formed. The pigment of the choroid is especially important in this respect; for the retina is very transparent, and if the surface behind it were not of a dark colour, but capable of reflecting the light, the luminous rays which had already acted on the retina would be reflected again through it, and would fall upon other parts of the same membrane, producing both dazzling from excessive light, and indistinctness of the images.

As an optical instrument, the eye is superior to the camera in the following, among many other particulars, which may be enumerated in detail. 1. The correctness of images even in a large field of view. 2. The simplicity and efficiency of the means by which chromatic aberration is avoided. 3. The perfect efficiency of its adaptation to different distances.

1. In the photographic camera, it is well-known that only a comparatively small object can be accurately focussed. In the photograph of a large object near at hand, the upper and lower limits are always more or less hazy, and vertical lines appear curved. This is due to the fact that the image produced by a

convex lens is really slightly curved and can only be received without distortion on a slightly curved concave screen, hence the distortion on a *flat* surface of ground glass. It is different with the eye, since it possesses a concave background, upon which the field of vision is depicted, and with which the curved form of the image coincides exactly. Thus, the defect of the camera obscura is entirely avoided; for the eye is able to embrace a large field of vision, the margins of which are depicted distinctly and without distortion. If the retina had a plane surface like the ground glass plate in a camera, it must necessarily be much larger than is really the case if we were to see as much; moreover, the central portion of the field of vision alone would give a good clear picture (Bernstein).

2. *Chromatic aberration.*—In the passage of light through an ordinary convex lens, decomposition of each ray into its elementary coloured parts commonly ensues, and a coloured margin appears around the image, owing to the unequal refraction which the elementary colours undergo. In the optical instruments this, which is termed *chromatic aberration*, is corrected by the use of two or more lenses, differing in shape and density, the second of which continues or increases the refraction of the rays produced by the first, but by recombining the individual parts of each ray into its original white light, corrects any chromatic aberration which may have resulted from the first. It is probable that the unequal refractive power of the transparent media in front of the retina may be the means by which the eye is enabled to guard against the effect of chromatic aberration. The human eye is achromatic, however, only so long as the image is received at its focal distance upon the retina, or so long as the eye adapts itself to the different distances of sight. If either of these conditions be interfered with, a more or less distinct appearance of colours is produced.

An ordinary ray of white light in passing through a prism, is refracted, *i.e.*, bent out of its course, but the different coloured rays which go to make up white light, are refracted in different degrees, and therefore appear as coloured bands fading off into each other: thus a coloured band known as the "spectrum" is

produced, the colours of which are arranged as follows,—red, orange, yellow, green, blue, indigo, violet; of these the red ray is the least, and the violet the most refracted. Hence, as Helmholtz has shown, a small white object cannot be accurately focussed on the retina, for if we focus for the red rays, the violet are out of focus, and *vice versâ*: such objects, if not exactly focussed, are often seen surrounded by a pale yellowish or bluish fringe.

For similar reasons a red surface looks nearer than a blue one at an equal distance, because the red rays being less refrangible, a stronger effort of accommodation is necessary to focus them, and the eye is adjusted as if for a nearer object, and therefore the red surface appears nearer.

From the insufficient adjustment of the image of a small white object, it appears surrounded by a sort of halo or fringe. This phenomenon is termed Irradiation. It is from this reason that a white square on a black ground appears larger than a black square of the same size on white ground.

3. *Accommodation of the Eye.*—The distinctness of the image formed upon the retina, is mainly dependent on the rays emitted by each luminous point of the object being brought to a perfect focus upon the retina. If this focus occur at a point either in front of, or behind the retina, indistinctness of vision ensues, with the production of a halo. The *focal distance*, *i.e.*, the distance of the point at which the luminous rays from a lens are collected, besides being regulated by the degree of convexity and density of the lens, varies with the distance of the object from the lens, being greater as this is shorter, and *vice versâ*. Hence, since objects placed at various distances from the eye can, within a certain range, different in different persons, be seen with almost equal distinctness, there must be some provision by which the eye is enabled to adapt itself, so that whatever length the focal distance may be, the focal point may always fall exactly upon the retina.

This power of *adaptation of the eye to vision at different distances* has received the most varied explanations. It is obvious that the effect might be produced in either of two ways, viz., by altering the convexity or density, and thus the refracting power, either of the cornea or lens; or, by

changing the position either of the retina or of the lens, so that whether the object viewed be near or distant, and the focal distance thus increased or diminished, the focal point to which the rays are converged by the lens may always be at the place occupied by the retina. The amount of either of these changes required in even the widest range of vision, is extremely small. For, from the refractive powers of the media of the eye, it has been calculated by Olbers, that the difference between the focal distances of the images of an object at such a distance that the rays are parallel, and of one at the distance of four inches, is only about 0·143 of an inch. On this calculation, the change in the distance of the retina from the lens required for vision at all distances, supposing the cornea and lens to maintain the same form, would not be more than about one line.

It is now almost universally believed that Helmholtz is right in his statement that the immediate cause of the adaptation of the eye for objects at different distances is a varying shape of the lens, its front surface becoming more or less convex, according to the distance of the object looked at. The nearer the object, the more convex does the front surface of the lens become, and *vice versâ;* the back surface taking little or no share in the production of the effect required.

The following simple experiment illustrates this point. If a small flame be held a little to one side of a person's eye, an observer looking at the eye from the other side sees three distinct images of the flame (fig. 311). The first and brightest is a small erect image (1) formed by the anterior convex surface of the cornea: the second (2) is also erect, but larger and less distinct than the preceding, it is formed at the anterior convex surface of the lens: the third (3) is smaller and reversed, it is formed at the posterior surface of the lens which is concave forwards and therefore, like all concave mirrors, gives a reversed image.

Fig. 311.*

If now the eye under observation be adjusted to a near object, the second image becomes smaller, clearer, and approaches the first: if the eye be adjusted for a far point, the second image enlarges again, becomes less distinct, and recedes from the first. In both cases alike the first and third images remain unaltered in size and relative position.

This proves that during accommodation for near objects the curvature of the cornea, and of the *posterior* of the lens, remains unaltered, while the *anterior* surface of the lens becomes more convex and approaches the cornea.

* Fig. 311. Diagram showing three reflections of a candle. 1, From the anterior surface of cornea; 2, from the anterior surface of lens; 3, from the posterior surface of lens. For further explanation see text.

Of course the lens has no inherent power of contraction, and therefore its changes of outline must be produced by some power from without; and there seems no reason to doubt that this power is supplied by the ciliary muscle. This muscle arises from the inner part of the sclerotic, just outside the margin of the cornea, from which it pulls as its fixed point. Its fibres are chiefly radiating and pass back to be inserted into the ciliary processes; there are also a few circular fibres. It is sometimes termed the *tensor choroideæ*. As this name implies, it draws forwards the choroid and therefore slackens the tension of the suspensory ligament of the lens which arises from it. The lens is usually partly flattened by the action of the suspensory ligament, and the ciliary muscle by diminishing the tension of this ligament diminishes, to a proportional degree, the flattening of which it is the cause. On diminution or cessation of the action of the ciliary muscle, the lens returns, in a corresponding degree, to its former shape, by virtue of the elasticity of its suspensory ligament.

In viewing near objects, the iris contracts, so that its pupillary edge is moved a very little forwards, and the pupil itself is contracted—the opposite effect taking place on withdrawal of the attention from near objects, and fixing it on those distant.

In every eye there is a limit to the power of accommodation. If a book be brought nearer and nearer to the eye, the type at last becomes indistinct and cannot be brought into focus by any effort of accommodation, however strong. This, which is termed the *near-point*, can be determined by the following experiment (Scheiner). Two small holes are pricked in a card with a pin; these should not be more than a line apart, at any rate their distance from each other must not exceed the diameter of the pupil. The card is held close in front of the eye, and a small needle viewed through the pin-holes. At a moderate distance it can be clearly focussed, but when brought nearer beyond a certain point, the image appears double or at any rate blurred. This point where the needle ceases to appear single is the near-point. Its distance from the eye can of course be readily measured. It is usually about 5 or 6 inches. In the accompanying figure (fig. 312) the lens *b* represents the eye; *ef*, the two pinholes in the card, *nn* the retina; *a* represents the position of the needle.

When the needle is at a moderate distance, the two pencils of light coming from *e* and *f*, are focussed at a single point on the retina *nn*. If the needle be brought nearer than the near-point, the strongest effort of accommo-

dation is not sufficient to focus the two pencils, they meet at a point behind the retina. The effect is the same as if the retina were shifted forward to *mm*. Two images *h.g*. are formed, one from each hole. It is interesting to note that when two images are produced, the lower one *g* really appears in the position Q, while the upper one appears in the position P. This may be readily verified by covering the holes in succession.

Fig. 312.*

Defects of Vision.—Under this head we may consider the defects known as Myopia, Hypermetropia, Presbyopia and Astigmatism.

The normal (emmetropic) eye is so adjusted that parallel rays are brought exactly to a focus on the retina without any effort of accommodation (1, fig. 313). Hence all objects except near ones (practically all objects more than twenty feet off) are seen without any effort of accommodation; in other words the far-point of the normal eye is at an infinite distance. In viewing near objects we are conscious of an effort (the contraction of the ciliary muscle) by which the anterior surface of the lens is rendered more convex, and rays which would otherwise be focussed *behind* the retina are converged upon the retina (see dotted lines 2, fig. 313).

1. *Myopia* (short-sight) (4, fig. 313).—This defect is due to an abnormal elongation of the eyeball. The eye is usually larger than normal and is always longer than normal; the lens is also probably too convex. The retina is too far from the lens and consequently parallel rays are focussed in front of the retina and crossing, form little circles on the retina; thus the images of distant objects are blurred and indistinct. The eye is, as it were, permanently adjusted for a near-point. Rays from a point

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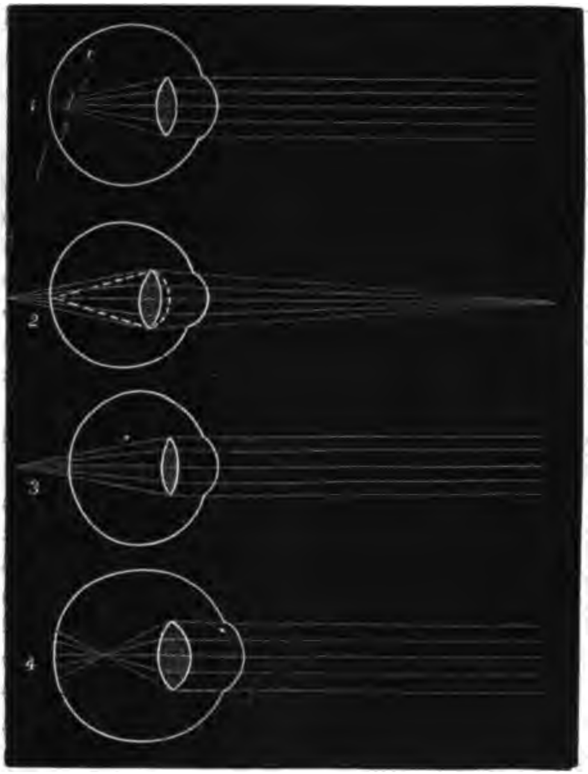
* Fig. 312. Diagram of experiment to ascertain the minimum distance of distinct vision. For explanation see text.

near the eye are exactly focussed in the retina. But those which issue from any object beyond a certain distance (far-point) cannot be distinctly focussed. This defect is corrected by

*Fig. 313.**



* Fig. 313. Diagrams showing—1, normal (emmetropic) eye, bringing parallel rays exactly to a focus on the retina; 2, normal eye adapted to a near-point; without accommodation the rays would be focussed behind the retina, but by increasing the curvature of the anterior surface of the lens (shown by a dotted line) the rays are focussed on the retina (as indicated by the meeting of the two dotted lines); 3, *hypermetropic* eye, in this case the axis of the eye is shorter, and the lens flatter, than normal; parallel rays are focussed behind the retina; 4, *myopic* eye; in this case the axis of the eye is abnormally long, and the lens too convex; parallel rays are focussed in front of the retina.

concave glasses which cause the rays entering the eye to diverge; hence they do not come to a focus so soon. Such glasses of course are only needed to give clear vision of distant objects. For near objects, except in extreme cases, they are not required.

2. *Hypermetropia* (long-sight) (3, fig. 313).—This is the reverse defect. The eye is too short and the lens too flat. Parallel rays are focussed *behind* the retina: an effort of accommodation is required to focus even parallel rays on the retina; and when they are divergent as in viewing a near object, the accommodation is insufficient to focus them. Thus in well-marked cases distant objects require an effort of accommodation and near ones a very powerful effort. Thus the ciliary muscle is constantly acting. This defect is obviated by the use of convex glasses which render the pencils of light more convergent. Such glasses are of course especially needed for near objects, as in reading, etc. They rest the eye by relieving the ciliary muscle from excessive work.

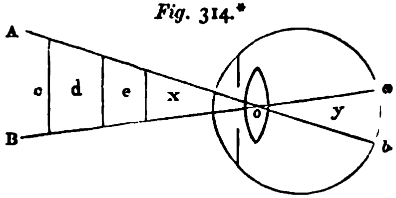
3. *Presbyopia*, which is frequently confounded with Hypermetropia, is really quite distinct. The former is an error of accommodation, the latter of refraction. Presbyopia is simply the gradual loss of the power of accommodation which is part of the general decay of old age. Thus a person who was hypermetropic in youth, but who by vigorous use of his accommodation could manage to see near objects, may become presbyopic in old age, *i.e.*, he may lose to a great extent control over his accommodation. In such a case he would be both hypermetropic and presbyopic at once. In reading he would be obliged to hold his book further and further away to focus the letters, till at last the letters are held too far for distinct vision. This condition is remedied by convex glasses, which are very commonly worn by old people.

4. *Astigmatism.*—This defect which was first discovered by Airy is due to a greater curvature of the eye in one meridian than in others. The eye may be even myopic in one plane and hypermetropic in others. Thus vertical and horizontal lines crossing each other cannot both be focussed at once; one set

stand out clearly and the others are blurred and indistinct. This defect which is present in a slight degree in all eyes may be corrected by the use of cylindrical glasses (*i.e.* curved only in one direction).

The direction given to the rays by their refraction is regulated by that of the central ray, or axis of the cone, towards which the rays are bent. The image of any point of an object is, therefore, as a rule (the exceptions to which need not here be stated), always formed in a line identical with the axis of the cone of light, as in the line of B *a*, or A *b*, (fig. 314), so that the spot where the image of any point will be formed upon the retina may be determined by prolonging the central ray of the cone of light, or that ray which traverses the centre of the pupil. Thus A *b* is the axis or central ray of the cone of light issuing from A; B *a*, the central ray of the cone of light issuing from B; the image of A is formed at *b*, the image of B at *a*, in the inverted position; therefore what in the object was above is in the image below, and *vice versâ*,—the right-hand part of the object is in the image to the left, the left-hand to the right. If an opening be made in an eye at its superior surface, so that the retina can be seen through the vitreous humour, this reversed image of any bright object, such as the windows of the room, may be perceived at the bottom of the eye. Or still better, if the eye of any albino animal, such as a white rabbit, in which the coats, from the absence of pigment, are transparent, is dissected clean, and held with the cornea towards a window, a very distinct image of the window completely inverted is seen depicted on the posterior translucent wall of the eye. Volkmann has also shown that a similar experiment may be successfully performed in a living person possessed of large prominent eyes, and an unusually transparent sclerotica.

Fig. 314.*



An image formed at any point on the retina is referred to a point outside the eye, lying on a straight line drawn from the

point on the retina outwards through the centre of the pupil. Thus an image on the left side of the retina is referred by the mind to an object on the right side of the eye, and *vice versâ*. Thus all images on the retina are mentally, as it were, projected in front of the eye, and the objects are seen *erect* though the image on the retina is *reversed*. Much needless confusion and difficulty has been raised on this subject for want of remembering that when we are said to *see* an object, the mind is merely conscious of the picture on the retina, and when it refers it to the external object or "projects" it outside the eye, it *necessarily* reverses it and sees the object as erect, though the retinal image is inverted. This is further corroborated by the sense of touch. Thus an object whose picture falls on the left half of the retina is reached by the right hand and hence is said to lie to the *right*. Or again, an object whose image is formed on the upper part of the retina is readily touched by the feet, and is therefore said to be in the *lower* part of the field, and so on.

Hence it is, also, that no discordance arises between the sensations of inverted vision and those of touch, which perceives everything in its erect position; for the images of all objects, even of our own limbs, in the retina, are equally inverted, and therefore maintain the same relative position.

Even the image of our hand, while used in touch, is seen inverted. The position in which we see objects, we call, therefore, the erect position. A mere lateral inversion of our body in a mirror, where the right hand occupies the left of the image, is indeed scarcely remarked: and there is but little discordance between the sensations acquired by touch in regulating our movements by the image in the mirror, and those of sight, as, for example, in tying a knot in the cravat. There is some want of harmony here, on account of the inversion being only lateral, and not complete in all directions.

The perception of the erect position of objects appears, therefore, to be the result of an act of the mind. And this leads us to a consideration of the several other properties of the retina, and of the co-operation of the mind in the several other parts of the act of vision. To these belong not merely the act of sensation itself, and the perception of the changes produced in the retina, as light and colours, but also the conversion of the mere

images depicted in the retina into ideas of an extended field of vision, of proximity and distance, of the form and size of objects, of the reciprocal influence of different parts of the retina upon each other, the simultaneous action of the two eyes, and some other phenomena.

To speak first of the *ideal size of the field of vision*.—The actual size of the field of vision depends on the extent of the retina, for only so many images can be seen at any one time as can occupy the retina, at the same time; and thus considered, the retina, of which the affections are perceived by the mind, is itself the field of vision. But to the mind of the individual the size of the field of vision has no determinate limits; sometimes it appears very small, at another time very large; for the mind has the power of projecting images on the retina towards the exterior. Hence the mental field of vision is very small when the sphere of the action of the mind is limited to impediments near the eye: on the contrary, it is very extensive when the projection of the images on the retina towards the exterior, by the influence of the mind, is not impeded. It is very small when we look into a hollow body of small capacity held before the eyes; large when we look out upon the landscape through a small opening; more extensive when we look at the landscape through a window; and most so when our view is not confined by any near object. In all these cases the idea which we receive of the size of the field of vision is very different, although its absolute size is in all the same, being dependent on the extent of the retina. Hence it follows, that the mind is constantly co-operating in the acts of vision, so that at last it becomes difficult to say what belongs to mere sensation, and what to the influence of the mind.

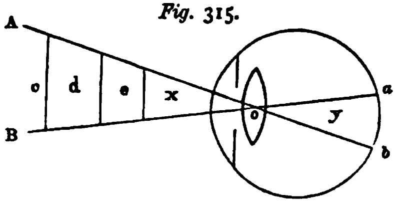
By a mental operation of this kind, we obtain a correct idea of the size of individual objects, as well as of the extent of the field of vision.

To illustrate this, it will be well to refer to fig. 315.

The angle x, included between the decussating central rays of two cones of light issuing from different points of an object, is called the optical angle —*angulus opticus seu visorius*. This angle becomes larger, the greater the distance between the points A and B; and since the angles x and y are

equal, the distance between the points *a* and *b* in the image on the retina increases as the angle *x* becomes larger. Objects at different distances from the eye, but having the same optical angle, *x*—for example, the objects, *c*, *d*, and *e*,—must also throw images of equal size upon the retina; and, if they occupy the same angle of the field of vision, their image must occupy the same spot in the retina.

Fig. 315.



Nevertheless, these images appear to the mind to be of very unequal size when the ideas of distance and proximity come into play; for, from the image *a b*, the mind forms the conception of a visual space extending to *e*, *d*, or *c*, and of an object of the size which that represented by the image on the retina appears to have when viewed close to the eye, or under the most usual circumstances.

Our estimate of the size of various objects is based partly on the visual angle under which they are seen, but much more on the estimate we form of their distance. Thus a lofty mountain many miles off may be seen under the same visual angle as a small hill near at hand, but we infer that the former is much the larger object because we know it is much further off than the hill. Our estimate of distance is often erroneous, and consequently the estimate of size also. Thus persons seen walking on the top of a small hill against a clear twilight sky appear unusually large, because we over-estimate their distance, and for similar reasons most objects in a fog appear immensely magnified. The same mental process gives rise to the idea of depth in the field of vision; this idea being fixed in our mind principally by the circumstance that, as we ourselves move forwards, different images in succession become depicted on our retina, so that we seem to pass between these images, which to the mind is the same thing as passing between the objects themselves.

The action of the sense of vision in relation to external objects is, therefore, quite different from that of the sense of touch. The objects of the latter sense are immediately present to it; and our own body, with which they come into contact, is the measure of their size. The part of a table touched by the hand appears as large as the part of the hand receiving an impression from it,

for a part of our body in which a sensation is excited, is here the measure by which we judge of the magnitude of the object. In the sense of vision, on the contrary, the images of objects are mere fractions of the objects themselves realised upon the retina, the extent of which remains constantly the same. But the imagination, which analyzes the sensations of vision, invests the images of objects, together with the whole field of vision in the retina, with very varying dimensions; the relative size of the images in proportion to the whole field of vision, or of the affected parts of the retina to the whole retina, alone remaining unaltered.

The direction in which an object is seen, the *direction of vision*, or *visual direction*, depends on the part of the retina which receives the image, and on the distance of this part from, and its relation to, the central point of the retina. Thus, objects of which the images fall upon the same parts of the retina lie in the same visual direction; and when, by the action of the mind, the images or affections of the retina are projected into the exterior world, the relation of the images to each other remains the same.

The estimation of the *form of bodies* by sight is the result partly of the mere sensation, and partly of the association of ideas. Since the form of the images perceived by the retina depends wholly on the outline of the part of the retina affected, the sensation alone is adequate to the distinction of only superficial forms of each other, as of a square from a circle. But the idea of a solid body, as a sphere, or a body of three or more dimensions, *e.g.*, a cube, can only be attained by the action of the mind constructing it from the different superficial images seen in different positions of the eye with regard to the object; and, as shown by Mr. Wheatstone and illustrated in the stereoscope, from two different perspective projections of the body being presented simultaneously to the mind by the two eyes. Hence, when, in adult age, sight is suddenly restored to persons blind from infancy, all objects in the field of vision appear at first as if painted flat on one surface; and no idea of solidity is formed until after long exercise of the sense of vision combined with that of touch.

The *clearness* with which an object is perceived irrespective of

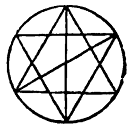
accommodation, would appear to depend largely on the number of rods and cones which its retinal image covers. Hence the nearer an object is to the eye (within moderate limits) the more clearly are all its details seen. Moreover, if we want carefully to examine any object, we always direct the eyes straight to it, so that its image shall fall on the yellow spot where an image of a given area will cover a larger number of cones than anywhere else in the retina. It has been found that the images of two points must be at least $\frac{1}{12000}$ in. apart on the yellow spot in order to be distinguished separately; if the images are nearer together, the points appear as one. The diameter of each cone in this part of the retina is about $\frac{1}{12000}$ in.

We judge of the *motion* of an object, partly from the motion of its image over the surface of the retina, and partly from the motion of our eyes following it. If the image upon the retina moves while our eyes and our body are at rest, we conclude that the object is changing its relative position with regard to ourselves. In such a case the movement of the object may be apparent only, as when we are standing upon a body which is in motion, such as a ship. If, on the other hand, the image does not move with regard to the retina, but remains fixed upon the same spot of that membrane, while our eyes follow the moving body, we judge of the motion of the object by the sensation of the muscles in action to move the eye. If the image moves over the surface of the retina while the muscles of the eye are acting at the same time in a manner corresponding to this motion, as in reading, we infer that the object is stationary, and we know that we are merely altering the relations of our eyes to the object. Sometimes the object appears to move when both object and eye are fixed, as in vertigo.

The mind can, by the faculty of *attention*, concentrate its activity more or less exclusively upon the senses of sight, hearing, and touch, alternately. When exclusively occupied with the action of one sense, it is scarcely conscious of the sensations of the others. The mind, when deeply immersed in contemplations of another nature, is indifferent to the actions of the sense of

sight, as of every other sense. We often, when deep in thought, have our eyes open and fixed, but see nothing, because of the stimulus of ordinary light being unable to excite the brain to perception, when otherwise engaged. The attention which is thus necessary for vision, is necessary also to analyse what the field of vision presents. The mind does not perceive all the objects presented by the field of vision at the same time with equal acuteness, but directs itself first to one and then to another. The sensation becomes more intense, according as the particular object is at the time the principal object of mental contemplation. Any compound mathematical figure produces a different impression according as the attention is directed exclusively to one or the other part of it. Thus in fig. 316, we may in succession have a vivid perception of the whole, or of distinct parts only; of the six triangles near the outer circle, of the hexagon in the middle, or of the three large triangles. The more numerous and varied the parts of which a figure is composed, the more scope does it afford for the play of the attention. Hence it is that architectural ornaments have an enlivening effect on the sense of vision, since they afford constantly fresh subject for the action of the mind.

Fig. 316.



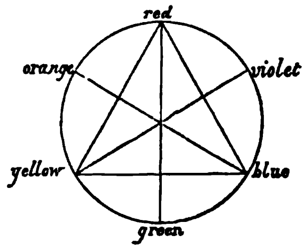
The *duration* of the sensation produced by a luminous impression on the retina is always greater than that of the impression which produces it. However brief the luminous impression, the effect on the retina always lasts for about one-eighth of a second. Thus, supposing an object in motion, say a horse, to be revealed on a dark night by a flash of lightning. The object would be seen apparently for an eighth of a second, but it would not appear in motion; because, although the image remained on the retina for this time, it was really revealed for such an extremely short period (a flash of lightning being almost instantaneous) that no appreciable movement on the part of the object could have taken place in the period during which it was revealed to the retina of the observer. And the same fact is proved in a reverse way. The spokes of a rapidly revolving wheel are not seen as distinct objects, because at every point of the field of

vision over which the revolving spokes pass, a given impression has not faded before another comes to replace it. Thus every part of the interior of the wheel appears occupied.

The duration of the *after-sensation* or *spectrum*, produced by an object, is greater in a direct ratio with the duration of the impression which caused it. Hence the image of a bright object, as of the panes of a window through which the light is shining, may be perceived in the retina for a considerable period, if we have previously kept our eye fixed for some time on it.

The colour of the spectrum varies with that of the object which produced it. The spectra left by the images of white or luminous objects, are ordinarily white or luminous; those left by dark objects are dark. Sometimes, however, the relation of the light and dark parts in the image may, under certain circumstances, be reversed in the spectrum; what was bright may be dark, and what was dark may appear light. This occurs whenever the eye, which is the seat of the spectrum of a luminous object, is not closed, but fixed upon another bright or white surface, as a white wall, or a

Fig. 317.*



* Fig. 317. A circle showing the various simple and compound colours of light, and those which are complemental of each other, *i.e.*, which, when mixed, produce a neutral grey tint. The three simple colours, red, yellow, and blue, are placed at the angles of an equilateral triangle; which are connected together by means of a circle; the mixed colours, green, orange, and violet, are placed intermediate between the corresponding simple or homogeneous colours; and the complemental colours, of which the pigments, when mixed, would constitute a grey, and of which the prismatic spectra would together produce a white light, will be found to be placed in each case opposite to each other, but connected by a line passing through the centre of the circle. The figure is also useful in showing the further shades of colour which are complementary of each other. If the circle be supposed to contain every transition of colour between the six marked down, those which, when united, yield a white or grey colour, will always be found directly opposite to each other; thus, for example, the intermediate tint between orange and red is complemental of the middle tint between green and blue.

sheet of white paper. Hence the spectrum of the sun, which, while light is excluded from the eye is luminous, appears black or grey when the eye is directed upon a white surface. The explanation of this is, that the part of the retina which has received the luminous image remains for a certain period afterwards in an exhausted or less sensitive state, while that which has received a dark image is in an unexhausted, and therefore much more excitable condition.

The ocular spectra which remain after the impression of coloured objects upon the retina are always coloured; and their colour is not that of the object, or of the image produced directly by the object, but the opposite, or *complemental* colour. The spectrum of a red object is, therefore, green; that of a green object, red; that of violet, yellow; that of yellow, violet, and so on. The reason of this is obvious. The part of the retina which receives, say, a red image, is wearied by that particular colour, but remains sensitive to the other rays which with red make up white light; and, therefore, these by themselves reflected from a white object produce a green hue. If, on the other hand, the first object looked at be green, the retina being tired of green rays, receives a red image when the eye is turned to a white object. And so with the other colours; the retina while fatigued by yellow rays will suppose an object to be violet, and *vice versâ;* the size and shape of the spectrum corresponding with the size and shape of the original object looked at. The colours which thus reciprocally excite each other in the retina are those placed at opposite points of the circle in fig. 317.

From these facts it would appear probable that the retina possesses special elements appropriated to special colours. The theory of Young and Helmholtz, according to which there are at least three such sets of elements for red, green, and violet, seems to be supported by the following facts. The peripheral parts of the retina have no perception of *red.* The area of the retina which is capable of receiving impressions of colour is slightly different for each colour. Again, *Daltonism* or colour-blindness is a by no means uncommon visual defect. One of the commonest forms is the inability to distinguish between red and

green and yellow. The simplest explanation of such a condition is that the elements of the retina which receive the impression of red, etc., are absent or very imperfectly developed.

Of the Reciprocal Action of Different Parts of the Retina on each other.

Although each elementary part of the retina represents a distinct portion of the field of vision, yet the different elementary parts, or sensitive points of that membrane, have a certain influence on each other; the particular condition of one influencing that of another, so that the image perceived by one part is modified by the image depicted in the other. The phenomena, which result from this relation between the different parts of the retina, may be arranged in two classes; the one including those where the condition existing in the greater extent of the retina is imparted to the remainder of that membrane; the other, consisting of those in which the condition of the larger portion of the retina excites, in the less extensive portion, the opposite condition.

1. When two opposite impressions occur in contiguous parts of an image on the retina, the one impression is, under certain circumstances, modified by the other. If the impressions occupy each one-half of the image, this does not take place; for in that case, their actions are equally balanced. But if one of the impressions occupies only a small part of the retina, and the other the greater part of its surface, the latter may, if long continued, extend its influence over the whole retina, so that the opposite less extensive impression is no longer perceived, and its place becomes occupied by the same sensation as the rest of the field of vision. Thus, if we fix the eye for some time upon a strip of coloured paper lying upon a white surface, the image of the coloured object, especially when it falls on the lateral parts of the retina, will gradually disappear, and the white surface be seen in its place.

2. In the second class of phenomena, the affection of one part of the retina influences that of another part, not in such a manner as to obliterate it, but so as to cause it to become the contrast or opposite of itself. Thus a grey spot upon a white ground appears darker than the same tint of grey would do if it alone occupied the whole field of vision, and a shadow is always rendered deeper when the light which gives rise to it becomes more intense, owing to the greater contrast.

The former phenomena ensue gradually, and only after the images have been long fixed on the retina; the latter are instantaneous in their production, and are permanent.

In the same way, also, colours may be produced by contrast. Thus, a very small dull-grey strip of paper, lying upon an extensive surface of any bright colour, does not appear grey, but has a faint tint of the colour which is the complement of that of the surrounding surface (see page 710). A strip of grey paper upon a green field, for example, often appears to have a tint of red, and when lying upon a red surface, a greenish tint; it has an orange-coloured tint upon a bright blue surface, and a bluish tint upon an orange-coloured surface; a yellowish colour upon a bright violet, and a violet tint upon a bright yellow surface. The colour excited thus, as a contrast to the exciting colour, being wholly independent of any rays of the corresponding colour acting from without upon the retina, must arise as an opposite or antagonistic condition of that membrane; and the opposite conditions of which the retina thus becomes the subject would seem to balance each other by their reciprocal reaction, A necessary condition for the production of the contrasted colours is, that the part of the retina in which the new colour is to be excited, shall be in a state of comparative repose; hence the small object itself must be grey. A second condition is, that the colour of the surrounding surface shall be very bright, that is, it shall contain much white light.

The Blind Spot.—The retina corresponding to the point of entrance of the optic nerve is completely insensible to the impressions of light. The phenomenon itself is very readily shown. If we direct one eye, the other being closed, upon a point at such a distance to the side of any object, that the image of the latter must fall upon the retina at the point of entrance of the optic nerve, this image is lost either instantaneously, or very soon. If, for example, we close the left eye, and direct the axis

of the right eye steadily towards the circular spot here represented, while the page is held at a distance of about six inches from the eye, both dot and cross are visible. On gradually increasing the distance between the eye and the object, by removing the book farther and farther from the face, and still keeping the right eye steadily on the dot, it will be found that suddenly the cross disappears from view, while on removing the book still farther, it suddenly comes in sight again. The cause of this phenomenon is simply that the portion of retina which is occupied by the entrance of the optic nerve, is quite blind; and therefore that when it alone occupies the field of vision, objects cease to be visible.

Of the Simultaneous Action of the two Eyes.

Although the sense of sight is exercised by two organs, yet the impression of an object conveyed to the mind is single.

Various theories have been advanced to account for this phenomenon. By Gall, it was supposed that we do not really employ both eyes simultaneously in vision, but always see with only one at a time. This especial employment of one eye in vision certainly occurs in persons whose eyes are of very unequal focal distance, but in the majority of individuals both eyes are simultaneously in action in the perception of the same object; this is shown by the double images seen under certain conditions. If two fingers be held up before the eyes, one in front of the other, and vision be directed to the more distant, so that it is seen singly, the nearer will appear double; while, if the nearer one be regarded, the most distant will be seen double; and one of the double images in each case will be found to belong to one eye, the other to the other eye.

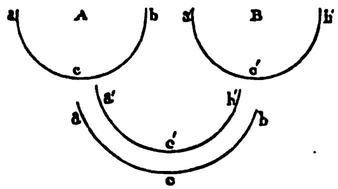
Single vision results only when certain parts of the two retinæ are affected simultaneously; if different parts of the retinæ receive the image of the object, it is seen double. This may be readily illustrated as follows:—The eyes are fixed upon some near object, and one of them is pressed by the thumb so as to be turned slightly in or out; two images of the object (*Diplopia* or Double Vision) are at once perceived, just as is frequently the case in persons who squint. This diplopia is due to the fact that the images of the object do not fall on corresponding points in the two retinæ.

The parts of the retinæ in the two eyes which thus correspond to each other in the property of referring the images which affect them simultaneously to the same spot in the field of vision are, in man, just those parts which would correspond to each other, if one retina were placed exactly in front of, and over the other (as in fig. 318, C). Thus, the outer lateral portion of one eye corresponds to, or, to use a better term, is identical with the inner portion of the other eye; or *a* of the eye A (fig. 318), with *a′* of the eye B. The upper part of one retina is also identical with the upper part of the other; and the lower parts of the two eyes are identical with each other.

This is proved by a simple experiment. Pressure upon any part of the ball of the eye, so as to affect the retina, produces a luminous circle, seen at the opposite side of the field of vision to that on which the pressure is made.

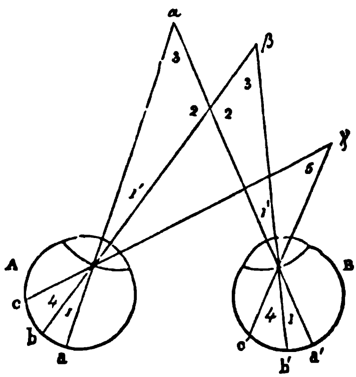
If, now, in a dark room, we press with the finger at the upper part of one eye, and at the lower part of the other, two luminous circles are seen, one above the other: so, also, two figures are seen when pressure is made simultaneously on the two outer or the two inner sides of both eyes. It is certain, therefore, that neither the upper part of one retina and the lower part of the other are identical, nor the outer lateral parts of the two retinæ, nor their inner lateral portions. But if pressure be made with the fingers upon both eyes simultaneously at their lower part, one luminous ring is seen at the middle of the upper part of the field of vision; if the pressure be applied to the upper part of both eyes, a single luminous circle is seen in the middle of the field of vision below. So, also, if we press upon the outer side *a* of the eye A, and upon the inner side *a′* of the eye B, a single spectrum is produced, and is apparent at the extreme right of the field of vision; if upon the point *b* of one eye, and the point *b′* of the other, a single spectrum is seen to the extreme left.

Fig. 318.



The spheres of the two retinæ may, therefore, be regarded as lying one over the other, as in C, fig. 318; so that the left portion of one eye lies over the identical left portion of the other eye, the right portion of one eye over the identical right portion of the other eye; and with the upper and lower portions of the two eyes, *a* lies over *a′*, *b* over *b′*, and *c* over *c′*. The points of the one retina intermediate between *a* and *c*, are again identical with the corresponding points of the other retina between *a′* and *c′*; those between *b* and *c* of the one retina, with those between *b′* and *c′* of the other. If the axes of the eyes, A and B (fig. 319), be so directed that they meet at *a*, an object at *a* will be seen singly, for the point *a* of the one retina, and *a′* of the other, are identical. So, also, if the object *β* be so situated that its image falls in both eyes at the same distance from the central point of the retina,—namely, at *b* in the one eye, and at *b′* in the other,—*β* will be seen single, for it affects identical parts of the two retinæ. The same will apply to the object *γ*.

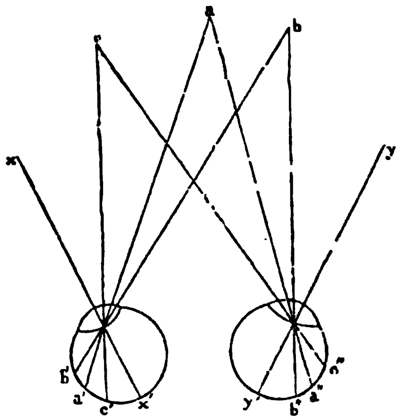
Fig. 319.



In quadrupeds, the relation between the identical and non-identical parts of the retinæ cannot be the same as in man; for the axes of their eyes generally diverge, and can never be made to meet in one point of an object.

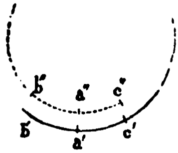
When an animal regards an object situated directly in front of it, the image of the object must fall, in both eyes, on the outer portion of the retinæ. Thus the image of the object *a* (fig. 320) will fall at *a′* in one, and at *a″* in

Fig. 320.



the other: and these points *a′* and *a″* must be identical. So, also, for distinct and single vision of objects, *b* or *c*, the points *b′* and *b″*, or *c′ c″*, in the two retinæ, on which the images of these objects fall, must be identical. All points of the retina in each eye which receive rays of light from lateral objects only, can have no corresponding identical points in the retina of the other eye; for otherwise two objects, one situated to the right and the other to the left, would appear to lie in the same spot of the field of vision. It is probable, therefore, that there are, in the eyes of animals, parts of the retinæ which are identical, and parts which are not identical, *i.e.*, parts in one which have no corresponding parts in the other eye. And the relation of the two retinæ to each other in the field of vision may be represented as in fig. 321.

Fig. 321.

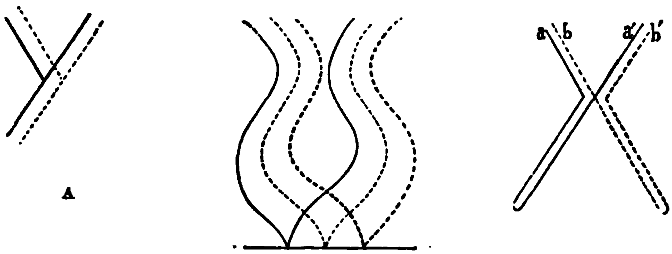


The cause of the impressions on the identical points of the two retinæ giving rise to but one sensation, and the perception of a single image, must either lie in the structural organization of the deeper or cerebral portion of the visual apparatus, or be the result of a mental operation; for in no other case is it the property of the corresponding nerves of the two sides of the body to refer their sensations as one to one spot.

Many attempts have been made to explain this remarkable relation between the eyes, by referring it to anatomical relation between the optic nerves. The circumstance of the inner portion of the fibres of the two optic nerves decussating at the commissure, and passing to the eye of the opposite side, while the outer portion of the fibres continue their course to the eye of the same side, so that the left side of both retinæ is formed from one root of the nerves, and the right side of both retinæ from the other root, naturally led to an attempt to explain the phenomenon by this distribution of the fibres of the nerves. And this explanation is favoured by cases in which the entire of one side of the retina, as far as the central point in both eyes, sometimes becomes insensible. But Müller shows the inadequateness of this theory to explain the phenomenon, unless it be supposed that each fibre in each cerebral portion of the optic nerves divides in the optic commissure into two branches for the identical points of the two retinæ, as is shown in A, fig. 322. But there is no foundation for such supposition.

By another theory it is assumed that each optic nerve contains exactly the same number of fibres as the other, and that the corresponding fibres of the two nerves are united in the Sensorium (as in fig. 322, B). But in this theory

Fig. 322.



A B C

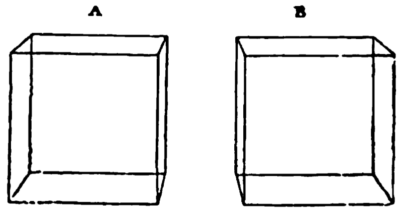
no account is taken of the partial decussation of the fibres of the nerves in the optic commissure.

According to a third theory, the fibres *a* and *a'*, fig. 322, C, coming from identical points of the two retinæ, are in the optic commissure brought into one optic nerve, and in the brain either are united by a loop, or spring from the same point. The same disposition prevails in the case of the identical fibres *b* and *b'*. According to this theory, the left half of each retina would be represented in the left hemisphere of the brain, and the right half of each retina in the right hemisphere.

Another explanation is founded on the fact, that at the anterior part of the commissure of the optic nerve, certain fibres pass across from the distal portion of one nerve to the corresponding portion of the other nerves, as if they were commissural fibres forming a connection between the retinæ of the two eyes. It is supposed, indeed, that these fibres may connect the corresponding parts of the two retinæ, and may thus explain their unity of action; in the same way that corresponding parts of the cerebral hemispheres are believed to be connected together by the commissural fibres of the corpus callosum, and so enabled to exercise unity of function.

On the whole, it is probable, that the power of forming a single idea of an object from a double impression conveyed by it to the eyes is the result of a mental act. This view is supported by the same facts as those employed by Professor Wheatstone to show that this power is subservient to the purpose of obtaining a right perception of bodies raised in relief. When an object is placed so near the eyes that to view it the optic axes must converge, a different perspective projection of it is seen by each eye, these perspectives being more dissimilar as the convergence of the optic axes becomes greater. Thus, if any figure of three dimensions, an outline cube, for example, be held at a moderate distance before the eyes, and viewed with each eye successively, while the head is kept perfectly steady, A (fig. 323) will be the

Fig. 323.



picture presented to the right eye, and B that seen by the left eye. Mr. Wheatstone has shown that on this circumstance depends in a great measure our conviction of the solidity of an object, or of its projection in relief. If different perspective drawings of a solid body, one representing the image seen by the right eye, the other that seen by the left (for example, the drawing of a cube, A, B, fig. 323), be presented to corresponding parts of the two retinæ, as may be readily done by means of the *stereoscope*, an instrument invented by Professor Wheatstone for the purpose, the mind will perceive not merely a single representation of the object, but a body projecting in relief, the exact counterpart of that from which the drawings were made.

By transposing two stereoscopic pictures a reverse effect is produced: the elevated parts appear to be depressed and *vice versâ*. An instrument contrived with this purpose is termed a

pseudoscope. Viewed with this instrument a bust appears as a hollow mask, and as may readily be imagined the effect is most bewildering.

CHAPTER XXII.

GENERATION AND DEVELOPMENT.

THE several organs and functions of the human body which have been considered in the previous chapters, have relation to the individual being. We have now to consider those organs and functions which are destined for the propagation of the species. These comprise the several provisions made for the formation, impregnation, and development of the ovum, from which the embryo or fœtus is produced and gradually perfected into a fully-formed human being.

The organs in the two sexes concerned in effecting these objects are named the Generative organs, or Sexual apparatus.

Generative Organs of the Female.

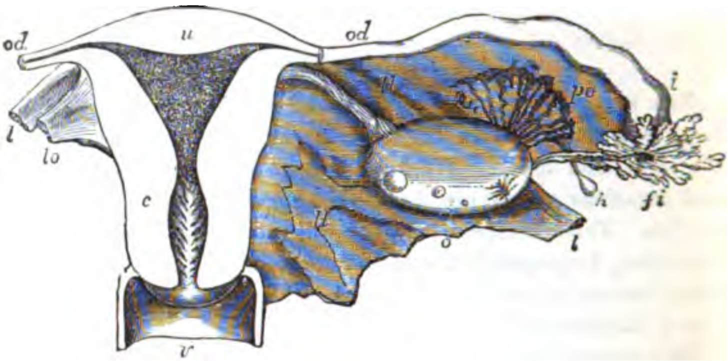
The female organs of generation (fig. 234) consist of two *Ovaries*, whose function is the formation of ova; of a *Fallopian tube*, or oviduct, connected with each ovary, for the purpose of conducting the ovum from the ovary to the *Uterus* or cavity in which, if impregnated, it is retained until the embryo is fully developed, and fitted to maintain its existence independently of internal connection with the parent; and, lastly, of a canal, or *vagina*, with its appendages, for the reception of the male generative organ in the act of copulation, and for the subsequent discharge of the fœtus.

The *ovaries* are two oval compressed bodies, situated in the cavity of the pelvis, one on each side, enclosed in the folds of the broad ligament. Each ovary measures about an inch and a half in length, three-quarters of an inch in width, and nearly half an inch in thickness, and is attached to the uterus by a narrow fibrous cord (the ligament of the ovary), and, more slightly, to

the Fallopian tube by one of the fimbriæ into which the walls of the extremity of the tube expand.

The ovary is enveloped by a *capsule* of dense fibro-cellular tissue, covered on the outside by epithelium, which, although

Fig. 324.*



continuous with, and originally derived from, the squamous epithelium of the peritoneum, is of columnar shape. The internal structure of the organ consists of a peculiar soft fibrous tissue, or *stroma*, abundantly supplied with blood-vessels, and having embedded in it, in various stages of development, numerous minute follicles or vesicles, the *Graafian vesicles*, or sacculi, containing the ova (fig. 325). (A further account of the Graafian vesicles and of their contained ova will be presently given.)

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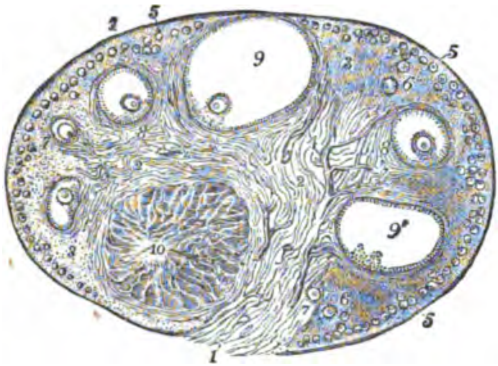
* Fig. 324. Diagrammatic view of the uterus and its appendages, as seen from behind. ½.—The uterus and upper part of the vagina have been laid open by removing the posterior wall; the Fallopian tube, round ligament, and ovarian ligament have been cut short, and the broad ligament removed on the left side; *u*, the upper part of the uterus; *c*, the cervix opposite the os internum; the triangular shape of the uterine cavity is shown, and the dilatation of the cervical cavity with the rugæ termed arbor vitæ; *v*, upper part of the vagina; *od*, Fallopian tube or oviduct; the narrow communication of its cavity with that of the cornu of the uterus on each side is seen; *l*, round ligament; *lo*, ligament of the ovary; *o*, ovary; *i*, wide outer part of the right Fallopian tube; *fi*, its fimbriated extremity; *po*, parovarium; *h*, one of the hydatids frequently found connected with the broad ligament (Allen Thomson).

The *Fallopian tubes* are about four inches in length, and extend between the ovaries and the upper angles of the uterus. At the point of attachment to the uterus, the Fallopian tube is

Fig. 325.*



very narrow; but in its course to the ovary it increases to about a line and a half in thickness; at its distal extremity, which is free and floating, it bears a number of *fimbriæ*, one of which, longer than the rest, is attached to the ovary. The canal by which each Fallopian tube is traversed is narrow, especially at its point of entrance into the uterus, at which it will scarcely admit a bristle; its other extremity is wider, and opens into the cavity of the abdomen, surrounded by the zone of fimbriæ. Externally, the Fallopian tube is invested with peritoneum; internally, its canal is lined with mucous membrane, covered

* Fig. 325. View of a section of the prepared ovary of the cat. 1, outer covering and free border of the ovary; 1′, attached border; 2, the ovarian stroma, presenting a fibrous and vascular structure; 3, granular substance lying external to the fibrous stroma; 4, blood-vessels; 5, ovigerms in their earliest stages occupying a part of the granular layer near the surface; 6, ovigerms which have begun to enlarge and to pass more deeply into the ovary; 7, ovigerms round which the Graafian follicle and tunica granulosa are now formed, and which have passed somewhat deeper into the ovary and are surrounded by the fibrous stroma; 8, more advanced Graafian follicle with the ovum imbedded in the layer of cells constituting the proligerous disc; 9, the most advanced follicle containing the ovum, etc.; 9′, a follicle from which the ovum has accidentally escaped; 10, corpus luteum (Schrön). $\frac{6}{1}$,

with ciliary epithelium: between the peritoneal and mucous coats, the walls are composed, like those of the uterus, of fibrous tissue and plain muscular fibres.

The *Uterus* (*u, c*, fig. 324) is somewhat pyriform, and in the unimpregnated state is about three inches in length, two in breadth at its upper part, or *fundus*, but at its lower pointed part or *neck*, only about half an inch. The part between the fundus and neck is termed the *body* of the uterus: it is about an inch in thickness.

The uterus is constructed of three principal layers, or coats,—*serous*, *fibro-cellular* and *muscular*, and *mucous*.

(1). The serous or peritoneal coat, which has the same general structure as the peritoneum, covers the organ before and behind, but is absent from the front surface of the neck.

(2) The middle coat is composed of dense connective tissue, with which are intermingled fibres of unstriped muscle. The latter become enormously developed during pregnancy.

(3). The mucous membrane of the uterus will be described more in detail presently (p. 759). It is lined by columnar ciliated epithelium, which extends also into the interior of the tubular glands, of which the mucous membrane is largely made up. (Allen Thomson, Nylander, Friedländer, John Williams.)

The cavity of the uterus corresponds in form to that of the organ itself: it is very small in the unimpregnated state; the sides of its mucous surface being almost in contact, and probably only separated from each other by mucus. Into its upper part, at each side, opens the canal of the corresponding Fallopian tube: below, it communicates with the vagina by a fissure-like opening in its neck, the *os uteri*, the margins of which are distinguished into two lips, an anterior and posterior. In the mucous membrane of the cervix are found several mucous follicles, termed ovula or glandulæ Nabothi: they probably form the jelly-like substance by which the os uteri is usually found closed.

The *vagina* is a membranous canal, five or six inches long, extending obliquely downwards and forwards from the neck of the uterus, which it embraces, to the external organs of genera-

tion. It is lined with mucous membrane, which in the ordinary contracted state of the canal is thrown into transverse folds. External to the mucous membrane, the walls of the vagina are constructed of fibro-cellular tissue, within which, especially around the lower part of the tube, is a layer of erectile tissue. The lower extremity of the vagina is embraced by an orbicular muscle, the *constrictor vaginæ*; its external orifice, in the virgin, is partially closed by a fold or ring of mucous membrane, termed the *hymen.* The external organs of generation consist of the *clitoris*, a small elongated body, situated above and in the middle line, and constructed, like the male penis, of two erectile corpora cavernosa, but unlike it, without a corpus spongiosum, and not perforated by the urethra; of two folds of mucous membrane, termed *labia interna*, or *nymphæ;* and, in front of these, of two other folds, the *labia externa*, or *pudenda*, formed of the external integument, and lined internally by mucous membrane. Between the nymphæ and beneath the clitoris is an angular space, termed the vestibule, at the centre of whose base is the orifice of the *meatus urinarius.* Numerous mucous follicles are scattered beneath the mucous membrane composing these parts of the external organs of generation; and at the side of the lower part of the vagina, are two larger lobulated glands, named *vulvo-vaginal*, or Duverney's glands, which are analogous to Cowper's glands in the male.

Unimpregnated Ovum.

If the *structure and formation* of the human ovary be examined at any period between early infancy and advanced age, but especially during that period of life in which the power of conception exists, it will be found to contain a number of small vesicles or membranous sacs of various sizes; these have been already alluded to as the *follicles* or *vesicles* of *De Graaf*, the anatomist who first accurately described them; they are also sometimes called *ovisacs.*

At their first formation, the Graafian vesicles, according to Schrön, are near the surface of the stroma of the ovary, but subsequently become more deeply placed; and again, as they increase in size, make their way towards the surface.

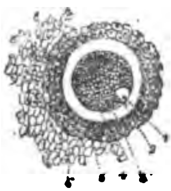
When mature, they form little prominences on the exterior of the ovary, covered only by a thin layer of condensed fibrous tissue and epithelium. Each follicle has an external membranous envelope, composed of fine fibro-cellular tissue, and connected with the surrounding stroma of the ovary by networks of blood-vessels. This envelope or tunic is lined with a layer of nucleated cells, forming a kind of epithelium or internal tunic, and named *membrana granulosa*. The cavity of the follicle is filled with an albuminous fluid in which microscopic granules float; and it contains also the *ovum*.

The ovum is a minute spherical body situated, in immature follicles, near the centre; but in those nearer maturity, in contact with the membrana granulosa at that part of the follicle which forms a prominence on the surface of the ovary. The cells of the membrana granulosa are at that point more numerous than elsewhere, and are heaped around the ovum, forming a kind of granular zone, the *discus proligerus* (fig. 326).

In order to examine an ovum, one of the Graafian vesicles, it matters not whether it be of small size or arrived at maturity, should be pricked, and the contained fluid received upon a piece of glass. The ovum then, being found in the midst of the fluid by means of a simple lens, may be further examined with higher microscopic powers. Owing to its globular form, however, its structure cannot be seen until it is subjected to gentle pressure.

The human ovum measures about $\frac{1}{120}$ of an inch. Its external investment is a transparent membrane, about $\frac{1}{2500}$ of an inch in thickness, which under the microscope appears as a bright ring (4, fig. 326), bounded externally and internally by a dark outline; it is called the *zona pellucida*, or *vitelline membrane*. It adheres externally to the heap of cells constituting the *discus proligerus*.

*Fig. 326.**



Within this transparent investment or zona pellucida, and usually in close contact with it, lies the yolk or vitellus, which is composed of granules and globules of various sizes, imbedded in a more or less fluid substance. The smaller granules, which are the

* Fig. 326. Ovum of the sow. 1. Germinal spot. 2. Germinal vesicle. 3. Yolk. 4. Zona pellucida. 5. Discus proligerus. 6. Adherent granules or cells (Barry).

more numerous, resemble in their appearance, as well as their constant motion, pigment-granules. The larger granules or globules which have the aspect of fat-globules, are in greatest number at the periphery of the yolk. The number of the granules is, according to Bischoff, greatest in the ova of carnivorous animals. In the human ovum their quantity is comparatively small.

In the substance of the yolk is imbedded the *germinal vesicle*, or vesicula germinativa (2, fig. 326). This vesicle is of greatest relative size in the smallest ova, and is in them surrounded closely by the yolk, nearly in the centre of which it lies. During the development of the ovum, the germinal vesicle increases in size much less rapidly than the yolk, and comes to be placed near to its surface. It is about $\frac{1}{720}$ of an inch in diameter. It consists of a fine, transparent, structureless membrane, containing a clear, watery fluid, in which are sometimes a few granules; and at that part of the periphery of the germinal vesicle which is nearest to the periphery of the yolk is situated the *germinal spot* (*macula germinativa*), a finely granulated substance, of a yellowish colour, strongly refracting the rays of light, and measuring about $\frac{1}{3000}$ of an inch in diameter.

Such are the parts of which the Graafian follicle and its contents, including the ovum, are composed. With regard to the mode and order of development of these parts there is considerable uncertainty; but it seems most likely that the ovum is formed before the Graafian vesicle or ovisac.

With regard to the parts of the *ovum* first formed, it appears certain that the formation of the germinal vesicle precedes that of the yolk and zona pellucida, or vitelline membrane. Whether the germinal spot is formed first, and the germinal vesicle afterwards developed around it, cannot be decided in the case of vertebrate animals; but the observations of Kölliker and Bagge on the development of the ova of intestinal worms show that in these animals, the first step in the process is the production of round bodies resembling the germinal spots of ova, the germinal vesicles being subsequently developed around these in the form of transparent membranous cells.

From the earliest infancy, and through the whole fruitful period of life, there appears to be a constant formation, development, and maturation of Graafian vesicles, with their contained ova. Until the period of puberty, however, the process is comparatively inactive; for, previous to this period, the ovaries are small and pale, the Graafian vesicles in them are very minute, and probably never attain full development, but soon shrivel and disappear, instead of bursting, as matured follicles do; the contained ova are also incapable of being impregnated. But, coincident with the other changes which occur in the body at the time of puberty, the ovaries enlarge, and become very vascular, the formation of Graafian vesicles is more abundant, the size and degree of development attained by them are greater, and the ova are capable of being fecundated.

Discharge of the Ovum.

In the process of development of individual Graafian vesicles, it has been already observed, that as each increases in size, it gradually approaches the surface of the ovary, and when fully ripe or mature, forms a little projection on the exterior. Coincident with the increase of size, caused by the augmentation of its liquid contents, the external envelope of the distended vesicle becomes very thin and eventually bursts. By this means, the ovum and fluid contents of the Graafian vesicle are liberated, and escape on the exterior of the ovary, whence they pass into the Fallopian tube, the fimbriated processes of the extremity of which are supposed coincidentally to grasp the ovary, while the aperture of the tube is applied to the part corresponding to the matured and bursting vesicle.

In animals whose capability of being impregnated occurs at regular periods, as in the human subject, and most Mammalia, the Graafian vesicles and their contained ova appear to arrive at maturity, and the latter to be discharged at such periods only. But in other animals, *e.g.*, the common fowl, the formation, maturation, and discharge of ova appear to take place almost constantly.

It has long been known, that in the so-called oviparous animals, the separation of ova from the ovary may take place independently of impregnation by the male, or even of sexual union. And it is now established that a like maturation and discharge of ova, independently of coition, occurs in Mammalia, the periods at which the matured ova are separated from the ovaries and received into the Fallopian tubes being indicated in the lower Mammalia by the phenomena of *heat* or *rut*: in the human female, although not always with exact coincidence, by the phenomena of *menstruation*. If the union of the sexes take place, the ovum may be fecundated, and if no union occur it perishes.

That this maturation and discharge occur periodically, and only during the phenomena of heat in the lower Mammalia, is made probable by the facts that, in all instances in which Graafian vesicles have been found presenting the appearance of recent rupture, the animals were at the time, or had recently been, in heat; that on the other hand, there is no authentic and detailed account of Graafian vesicles being found ruptured in the intervals of the periods of heat; and that female animals do not admit the males, and never become impregnated, except at those periods.

Many circumstances make it certain that the human female is subject, in these respects, to the same law as the females of other mammiferous animals; namely, that in her as in them, ova are matured and discharged from the ovary independent of sexual union. This maturation and discharge occur, moreover, periodically at or about the epochs of menstruation. Thus Graafian vesicles recently ruptured have been frequently seen in ovaries of virgins or women who could not have been recently impregnated; and although it is true that the ova discharged under these circumstances have rarely been discovered in the Fallopian tube,* partly on account of their minute size, and partly because the search has seldom been prosecuted with much care, yet analogy forbids us to doubt that in the human female, as in the domestic

* See, however, the record of two such cases by Dr. Letheby, in the Philosophical Transactions, 1851.

quadrupeds, the result and purpose of the rupture of the follicles is the discharge of the ova.

The evidence of the periodical discharge of ova is that in most cases in which signs of menstruation have been found in the uterus, follicles in a state of maturity or of rupture have been seen in the ovary; and that although conception is not confined to the periods of menstruation, yet it is more likely to occur about a menstrual epoch than at other times.

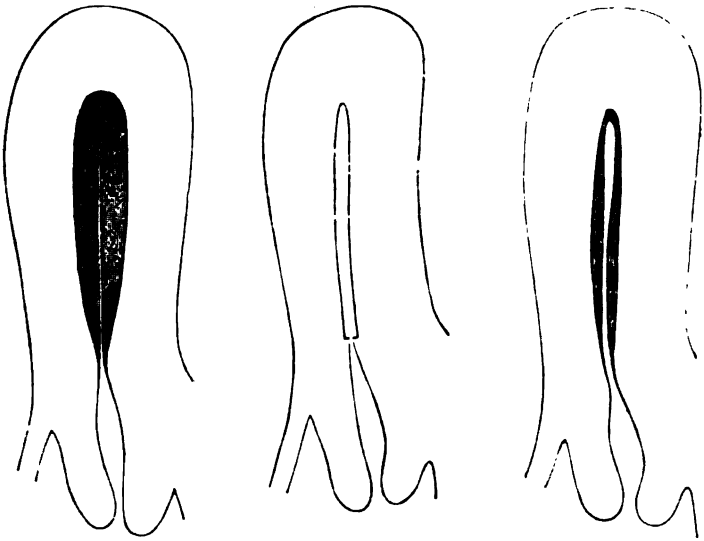
The exact relation between the discharge of ova and menstruation is not very clear. It was generally believed that the monthly flux was the result of a congestion of the uterus arising from the enlargement and rupture of a Graafian follicle, but though a Graafian follicle is, as a rule, ruptured at each menstrual epoch, yet several instances are recorded in which menstruation has occurred where no Graafian follicle has been ruptured, and on the other hand cases are known where ova have been discharged in amenorrhœic women. It must therefore be admitted that menstruation is not dependent on the maturation and discharge of ova.

It was, moreover, generally understood that ova were discharged towards the close or soon after the cessation of a menstrual flow. Observations made after death, and facts obtained by clinical investigation, however, do not support this view. (Reichert, J. Williams, Löwenthal.) Rupture of a Graafian follicle does not happen on the same day of the monthly period in all women. It may occur towards the close or soon after the cessation of a flow; but only in a small minority of the subjects examined after death was this the case. On the other hand, in almost all such subjects of which there is record, rupture of the follicle appears to have taken place before the commencement of the catamenial flow. Moreover, the custom of the Jews—a prolific race, to whom by the Levitical law sexual intercourse during the week following menstruation was forbidden—militates strongly in favour of the view that conception usually occurs before and not soon after a menstrual epoch, and necessarily, therefore, for the view that ova are usually discharged before the catamenial flow. This, together with the anatomical condition of the uterus just before the

catamenia, seem to indicate that the ovum fertilized is that which is discharged in connection with the first absent, and not that with the last present menstruation. (Kundrat.)

Though menstruation does not appear to depend upon the discharge of ova, yet the presence of the ovaries seems necessary for the performance of the function; for women do not menstruate when both ovaries have been removed by operation, as in the case recorded by Pott. Some instances have been recently recorded, indeed, of a sanguineous discharge, occurring periodically from the vagina after both ovaries have been previously removed for disease; and it has been inferred from this that menstruation is a function independent of the ovary; but this evidence is not conclusive, inasmuch as it is possible that portions of ovarian tissue were left after the operation.

Fig. 327.* *Fig.* 328. *Fig.* 329.



* Fig. 327. Diagram of uterus just before menstruation; the shaded portion represents the thickened mucous membrane. Fig. 328. Diagram of uterus when menstruation has just ceased, showing the cavity of the uterus deprived of mucous membrane. Fig. 329. Diagram of uterus a week after the menstrual flux has ceased: the shaded portion represents renewed mucous membrane (J. Williams).

The menstrual discharge is a thin sanguineous fluid, having a peculiar odour. It is of a dark colour, and consists of blood, epithelium, and mucus from the uterus and vagina, serum, and the débris of a membrane called the *decidua menstrualis*.

This membrane is the developed mucous surface of the body of the uterus. It does not extend into the Fallopian tube or into the cavity of the cervix. It attains its highest state of development in the unimpregnated organ just before the commencement of a catamenial flow (fig. 327). If impregnation take place, it becomes the *decidua vera;* if impregnation fail, the membrane undergoes rapid disintegration; its vessels are laid open and hæmorrhage follows (John Williams). The blood poured out does not coagulate in consequence of the admixture already mentioned; or, very possibly, coagulation occurs, but the process is more or less spoiled, and what clot is formed is almost at once broken down again, so as to imitate liquid blood. (See also p. 107.)

Menstruation, therefore, is not the result of congestion, or of a species of erection, but of a destructive process by which the *decidua* or *nidus* prepared for an impregnated ovum is carried away. It is not a sign of the capability of being impregnated as much as of disappointed impregnation.

The occurrence of a menstrual discharge is one of the most prominent indications of the commencement of puberty in the female sex; though its absence even for several years is not necessarily attended with arrest of the other characters of this period of life, or with inaptness for sexual union, or incapability of impregnation. The average time of its first appearance in females of this country and others of about the same latitude, is from fourteen to fifteen; but it is much influenced by the kind of life to which girls are subjected, being accelerated by habits of luxury and indolence, and retarded by contrary conditions. On the whole, its appearance is earlier in persons dwelling in warm climes than in those inhabiting colder latitudes; though the extensive investigations of Mr. Robertson show that the influence of temperature on the development of puberty has been exaggerated. Much of the influence attributed to climate appears due

to the custom prevalent in many hot countries, as in Hindostan, of giving girls in marriage at a very early age, and inducing sexual excitement previous to the proper menstrual time. The menstrual functions continue through the whole fruitful period of a woman's life, and usually cease between the forty-fifth and fiftieth years.

The several menstrual periods usually occur at intervals of a lunar month, the duration of each being from three to six days. In some women the intervals are as short as three weeks or even less; while in others they are longer than a month. The periodical return is usually attended by pain in the loins, a sense of fatigue in the lower limbs, and other symptoms, which are different in different individuals. Menstruation does not usually occur in pregnant women, or in those who are suckling; but instances of its occurrence in both these conditions are by no means rare.

Corpus Luteum.

Immediately before, as well as subsequent to, the rupture of a Graafian vesicle, and the escape of its ovum, certain changes ensue in the interior of the vesicle, which result in the production of a yellowish mass, termed a *corpus luteum.*

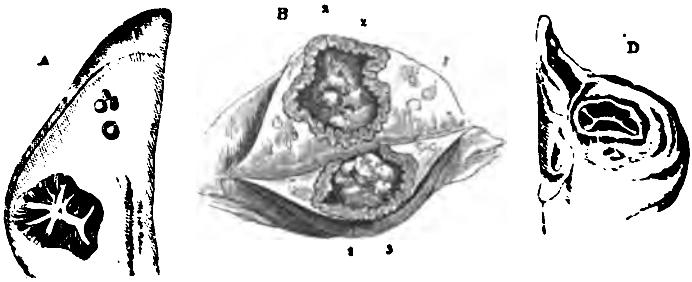
When fully formed the corpus luteum of mammiferous animals is a roundish solid body, of a yellowish or orange colour, and composed of a number of lobules, which surround, sometimes a small cavity, but more frequently a small stelliform mass of white substance, from which delicate processes pass as septa between the several lobules. Very often, in the cow and sheep, there is no white substance in the centre of the corpus luteum; and the lobules projecting from the opposite walls of the Graafian vesicle appear in a section to be separated by the thinnest possible lamina of semi-transparent tissue.

When a Graafian vesicle is about to burst and expel the ovum, it becomes highly vascular and opaque; and, immediately before the rupture takes place, its walls appear thickened on the interior by a reddish glutinous or fleshy-looking substance. Immediately after the rupture, the inner layer of the wall of the

vesicle appears pulpy and flocculent. It is thrown into wrinkles by the contraction of the outer layer, and, soon, red fleshy mammillary processes grow from it, and gradually enlarge till they nearly fill the vesicle, and even protrude from the orifice in the external covering of the ovary. Subsequently this orifice closes, but the fleshy growth within still increases during the earlier period of pregnancy, the colour of the substance gradually changing from red to yellow, and its consistence becoming firmer.

The corpus luteum of the human female (fig. 330) differs from that of the domestic quadruped in being of a firmer texture, and having more frequently a persistent cavity at its

Fig. 330.*



centre, and in the stelliform cicatrix, which remains in the cases where the cavity is obliterated, being proportionately of much larger bulk. The quantity of yellow substance formed is also much less: and, although the deposit increases after the vesicle has burst, yet it does not usually form mammillary growths projecting into the cavity of the vesicle, and never protrudes from the orifice, as is the case in other Mammalia. It maintains the character of a uniform, or nearly uniform, layer, which is thrown into wrinkles, in consequence of the contraction of the

* Fig. 330. Corpora lutea of different periods. B. Corpus luteum of about the sixth week after impregnation, showing its plicated form at that period. 1. Substance of the ovary. 2. Substance of the corpus luteum. 3. A greyish coagulum in its cavity (Paterson). A. Corpus luteum two days after delivery. D. In the twelfth week after delivery (Montgomery).

external tunic of the vesicle. After the orifice of the vesicle has closed, the growth of the yellow substance continues during the first half of pregnancy, till the cavity is reduced to a comparatively small size, or is obliterated; in the latter case, merely a white stelliform cicatrix remains in the centre of the corpus luteum.

An effusion of blood generally takes place into the cavity of the Graafian vesicle at the time of its rupture, especially in the human subject; but it has no share in forming the yellow body; it gradually loses its colouring matter, and acquires the character of a mass of fibrin. The serum of the blood sometimes remains included within a cavity in the centre of the coagulum, and then the decolorized fibrin forms a membraniform sac, lining the corpus luteum. At other times the serum is removed, and the fibrin constitutes a solid stelliform mass.

The yellow substance of which the corpus luteum consists, both in the human subject and in the domestic animals, is a growth from the inner surface of the Graafian vesicle, the result of an increased development of the cells forming the membrana granulosa, which naturally lines the internal tunic of the vesicle.

The first changes of the internal coat of the Graafian vesicle in the process of formation of a corpus luteum, seem to occur in every case in which an ovum escapes; as well in the human subject as in the domestic quadrupeds. If the ovum is impregnated, the growth of the yellow substance continues during nearly the whole period of gestation and forms the large corpus luteum commonly described as a characteristic mark of impregnation. If the ovum is not impregnated, the growth of yellow substance on the internal surface of the vesicle proceeds, in the human ovary, no further than the formation of a thin layer, which shortly disappears; but in the domestic animals it continues for some time after the ovum has perished, and forms a corpus luteum of considerable size. The fact, that a structure, in its essential characters similar to, though smaller than, a corpus luteum observed during pregnancy, is formed in the human subject, independent of impregnation or of sexual union, coupled with the varieties in size of corpora lutea formed during

pregnancy, necessarily renders unsafe all evidence of previous impregnation founded on the existence of a corpus luteum in the ovary.

The following table by Dalton, expresses well the differences between the corpus luteum of the pregnant and unimpregnated condition respectively.

	Corpus Luteum of Menstruation.	Corpus Luteum of Pregnancy.
At the end of three weeks.	Three-quarters of an inch in diameter; central clot reddish; convoluted wall pale.	
One month .	Smaller; convoluted wall bright yellow; clot still reddish.	Larger; convoluted wall bright yellow; clot still reddish.
Two months .	Reduced to the condition of an insignificant cicatrix.	Seven-eighths of an inch in diameter; convoluted wall bright yellow; clot perfectly decolorised.
Six months .	Absent.	Still as large as at end of second month; clot fibrinous; convoluted wall paler.
Nine months .	Absent.	One-half an inch in diameter; central clot converted into a radiating cicatrix; the external wall tolerably thick and convoluted, but without any bright yellow colour.

IMPREGNATION OF THE OVUM.

Male Sexual Functions.

The fluid of the male, by which the ovum is impregnated, consists essentially of the semen secreted by the *testicles*: and to this are added, as necessary, perhaps, to its perfection, a material secreted by the *vesiculæ seminales* (in which, as in reservoirs, the semen lies before its discharge), as well as the secretion of the prostate gland, and of Cowper's glands. Portions of these several fluids are, probably, all discharged, together with the proper secretion of the testicles.

The secreting structure of the testicle and its duct are disposed in two contiguous parts, (1) the body of the testicle enclosed within a tough fibrous membrane, the *tunica albuginea*, on the outer surface of which is the serous covering formed by the *tunica vaginalis*, and (2) the *epididymis* and *vas deferens*.

The *vas deferens*, or duct of the testicle, which is about two feet in length, is constructed externally of connective tissue, and internally is lined by mucous membrane, covered by columnar epithelium; while between these two coats is a middle coat, very firm and tough, made up chiefly of longitudinal with some circular plain muscular fibres. When followed back to its origin, the vas deferens is found to pass to the lower part of the *epididymis*, with which it is directly continuous (fig. 333), and assumes there a much smaller diameter with an exceedingly tortuous course.

Fig. 331.*

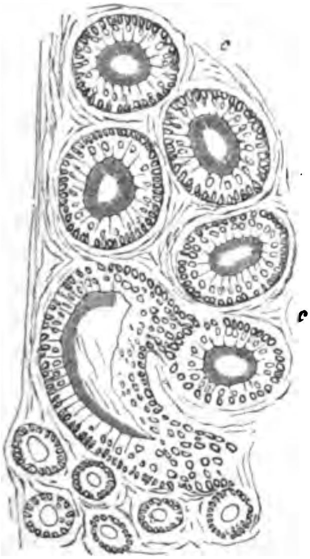
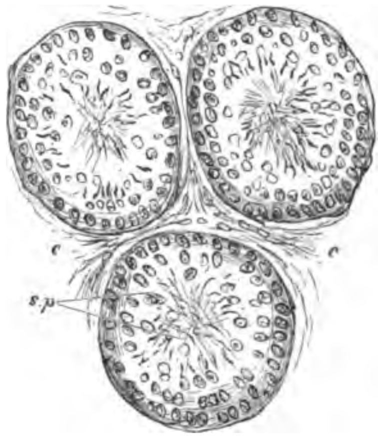


Fig. 332.†



The *epididymis*, which is lined, except at its lowest part, by

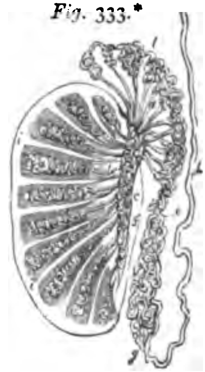
* Fig. 331. Section of dog's epididymis. The tube is cut in several places, both transversely and obliquely; it is seen to be lined by a ciliated epithelium, the nuclei of which are well shown. *c*, connective tissue (Schofield).

† Fig. 332. A section of dog's testicle highly magnified, showing three "tubuli seminiferi," lined and largely occupied by a spheroidal epithelium, the numerous nuclei of which are well seen; *c*, connective tissue surrounding and supporting the tubuli; *sp*, masses of spermatozoa occupying the centre of tubuli: the small black bodies scattered about are the heads of the spermatozoa (Schofield).

columnar ciliated epithelium (fig. 331), is commonly described as consisting (fig. 333) of a *globus minor* (*g*), the *body* (*e*), and the *globus major* (*l*). When unravelled, it is found to be constructed of a single tube, measuring about twenty feet in length.

At the globus major this duct divides into ten or twelve small branches, the convolutions of which form coniform masses, named *coni vasculosi;* and the ducts continued from these, the *vasa efferentia,* after anastomosing, one with another, in what is called the *rete testis,* lead finally as the *tubuli recti* or *vasa recta* to the *tubules* which form the proper substance of the testicle, wherein they are arranged in lobules, closely packed, and all attached to the tough fibrous tissue at the back of the testicle. The epithelium of the coni vasculosi and vasa efferentia is columnar and ciliated; that of the rete testis is squamous.

Fig. 333.*



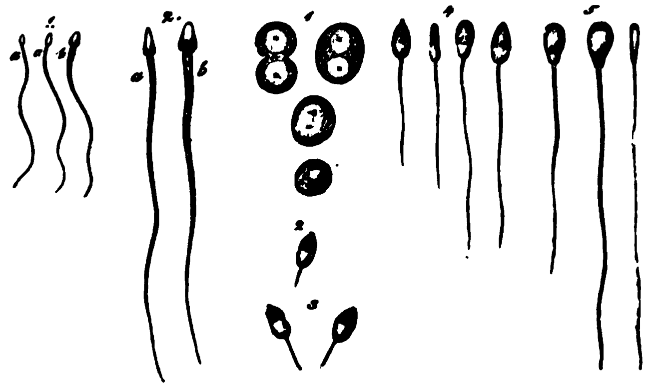
The *seminal tubes,* or *tubuli seminiferi,* which compose the proper substance of the testicle, are fine thread-like tubules, formed of simple homogeneous membrane, measuring on an average $\frac{1}{100}$th to $\frac{1}{200}$th of an inch in diameter, and lined with spheroidal epithelium (fig. 332). Rarely branching, they extend as simple tubes through a great length, with the same uniform structure, and terminate either in free closed extremities or in loops. Their walls are covered with fine capillary blood-vessels, through which, reckoning their great extent in comparison with the size of the spermatic artery, the blood must move very slowly.

The *seminal fluid* secreted by the testicle is one of those secretions in which a process of development is continued after its

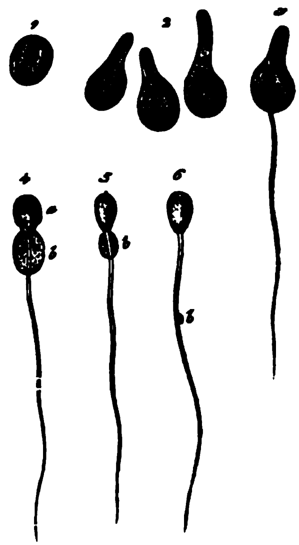
* Fig. 333. Plan of a vertical section of the testicle, showing the arrangement of the ducts. The true length and diameter of the ducts have been disregarded. *a, a,* tubuli seminiferi coiled up in the separate lobes; *b,* tubuli recti or vasa recta; *c,* rete testis; *d,* vasa efferentia ending in the coni vasculosi; *l, e, g,* convoluted canal of the epididymis; *h,* vas deferens; *f,* section of the back part of the tunica albuginea; *i, i,* fibrous processes running between the lobes; *s,* mediastinum.

formation by the secreting cells, and its discharge from them into the tubes. The principal part of this development consists

A *Fig.* 334.* B



C



in the formation of the peculiar bodies named *seminal filaments* or *spermatozoa* (fig. 334), the complete development of which, in their full proportion or number, is not

* Fig. 334. A, spermatic filaments from the human vas deferens (from Kölliker). 1, magnified 350 diameters; 2, magnified 800 diameters; *a*, from the side; *b*, from above. B, spermatic cells and spermatozoa of the bull undergoing development (from Kölliker) $\frac{450}{1}$. 1, spermatic cells, with one or two nuclei, one of them clear; 2, 3, free nuclei, with spermatic filaments forming; 4, the filaments elongated and the body widened; 5, filaments nearly fully developed. C, escape of the spermatozoa from their cells in the same animal. 1, spermatic cell containing the spermatozoon coiled up within it; 2, the cells elongated by the partial uncoiling of the spermatic filament; 3, a cell from which the filament has in part become free; 4, the same with the body also partially free; 5, spermatozoon from the epididymis with vestiges of the cell adherent; 6, spermatozoon from the vas deferens, showing the small enlargement, *b*, on the filament.

achieved till the semen has reached, or has for some time lain in, the vesiculæ seminales. Earlier, after its first secretion, the semen contains none of these bodies, but granules and round corpuscles (seminal corpuscles), like large nuclei, enclosed within parent-cells (fig. 213, B, 1). Within each of these corpuscles, or nuclei, a seminal filament is developed, by a similar process in nearly all animals. Each corpuscle, or nucleus, is filled with granular matter; this is gradually converted into a spermatozoon, which is at first coiled up, and in contact with the inner surface of the wall of the corpuscle (fig. 334, C, 1).

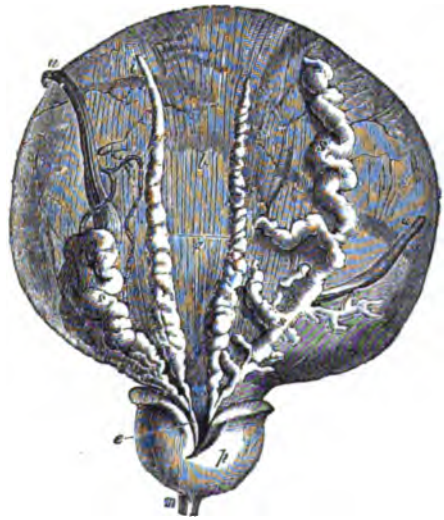
Thus developed, the human seminal filaments consist of a long, slender, tapering portion, called the body or tail, to distinguish it from the head, an oval or pyriform portion of larger diameter, flattened, and sometimes pointed. They are from $\frac{1}{500}$th to $\frac{1}{600}$th of an inch in length, the length of the head alone being from $\frac{1}{5000}$th to $\frac{1}{3000}$th of an inch, and its width about half as much. They present no trace of structure, or dissimilar organs; a dark spot often observed in the head, is probably due to its being concave, like a blood corpuscle. They move about in the fluid like so many minute tadpoles, lashing their tails, and propelling their heads forwards in various lines. Their movement, which is probably essentially, as well as apparently, similar to that of ciliary processes, appears nearly independent of external conditions, provided the natural density of the fluid is preserved; disturbing this condition, by either evaporating the semen or diluting it, will stop the movement. It may continue within the body of the female for seven or eight days, and out of the body for at least nearly twenty-four hours. The direction of the movement is quite uncertain: but in general, the current that each excites keeps it from the contact of others. The rate of motion, according to Valentin, is about one inch in thirteen minutes.

The occurrence of spermatozoa in the impregnating fluid of nearly all classes of animals, proves that they are essential to the process of impregnation, and their actual contact with the ovum is necessary for its development; but concerning the manner of their action nothing is known.

The seminal fluid is, probably, after the period of puberty, secreted constantly, though, except under excitement, very slowly, in the tubules of the testicles. From these it passes along the vasa deferentia into the vesiculæ seminales, whence, if not expelled in emission, it may be discharged, as slowly as it enters them, either with the urine, which may remove minute quantities, mingled with the mucus of the bladder and the secretion of the prostate, or from the urethra in the act of defæcation.

The *vesiculæ seminales* (fig. 335) have the appearance of outgrowths from the vasa deferentia. Each vas deferens, just before it enters the prostate gland, through part of which it

Fig. 335.*



* Fig. 335. Dissection of the base of the bladder and prostate gland, showing the vesiculæ seminales and vasa deferentia (Haller).—*a*, lower surface of the bladder at the place of reflexion of the peritoneum; *b*, the part above covered by the peritoneum; *i*, left vas deferens, ending in *e*, the ejaculatory duct; the vas deferens has been divided near *i*, and all except the vesicle portion has been taken away; *s*, left vesicula seminalis joining the same duct; *s*, *s*, the right vas deferens and right vesicula seminalis, which has been unravelled; *p*, under side of the prostate gland; *m*, part of the urethra; *u*, *u*, the ureters (cut short), the right one turned aside.

passes to terminate in the urethra, gives off a side-branch, which bends back from it at an acute angle; and this branch dilating, variously branching, and pursuing in both itself and its branches a tortuous course, forms the vesicula seminalis. Each of the vesiculæ, therefore, might be unravelled into a single branching tube, sacculated, convoluted, and folded up. Tho structure of the vesiculæ resembles closely that of the vasa deferentia.

The mucous membrane lining the vesiculæ seminales, like that of the gall-bladder, is minutely wrinkled and set with folds and ridges arranged so as to give it a finely reticulated appearance.

To the vesiculæ seminales a double function may be assigned; for they both secrete some fluid to be added to that of the testicles, and serve as reservoirs for the seminal fluid. The former is their most constant and probably most important office; for in the horse, bear, guinea-pig, and several other animals, in whom the vesiculæ seminales are large and of apparently active function, they do not communicate with the vasa deferentia, but pour their secretions, separately, though it may be simultaneously, into the urethra. In man, also, when one testicle is lost, the corresponding vesicula seminalis suffers no atrophy, though its function as a reservoir is abrogated. But how the vesiculæ seminales act as secreting organs is unknown; the peculiar brownish fluid which they contain after death does not properly represent their secretion, for it is different in appearance from anything discharged during life, and is mixed with semen. It is nearly certain, however, that their secretion contributes to the proper composition of the impregnating fluid; for in all the animals in whom they exist, and in whom the generative functions are exercised at only one season of the year, the vesiculæ seminales, whether they communicate with the vasa deferentia or not, enlarge commensurately with the testicles at the approach of that season.

That the vesiculæ are also reservoirs in which the seminal fluid may lie for a time previous to its discharge, is shown by their commonly containing the seminal filaments in larger abundance than any portion of the seminal ducts themselves do. The uid-like mucus, also, which is often discharged from the vesi-

culæ in straining during defæcation, commonly contains seminal filaments. But no reason can be given why this office of the vesiculæ should not be equally necessary to all the animals whose testicles are organised like those of man, or why in many animals the vesiculæ are wholly absent.

There is an equally complete want of information respecting the secretions of the prostate and Cowper's glands, their nature and purposes. That they contribute to the right composition of the impregnating fluid, is shown both by the position of the glands and by their enlarging with the testicles at the approach of an animal's breeding time. But that they contribute only a subordinate part is shown by the fact, that, when the testicles are lost, though these other organs be perfect, all procreative power ceases.

The Semen.

The mingled secretions of all the organs just described, form the *semen* or seminal fluid. Its corpuscles have been already described (p. 738): its fluid part has not been satisfactorily analysed: but Henle says it contains fibrin, because shortly after being discharged, flocculi form in it by spontaneous coagulation, and leave the rest of it thinner and more liquid, so that the filaments move in it more actively.

Nothing has shown what it is that makes this fluid with its corpuscles capable of impregnating the ovum, or (what is yet more remarkable) of giving to the developing offspring all the characters, in features, size, mental disposition, and liability to disease, which belong to the father. This is a fact wholly inexplicable: and is, perhaps, only exceeded in strangeness by those facts which show that the seminal fluid may exert such an influence, not only on the ovum which it impregnates, but, through the medium of the mother, on many which are subsequently impregnated by the seminal fluid of another male.

It has been often observed that a well-bred bitch, if she have been once impregnated by a mongrel dog, will not bear thorough-bred puppies in the next two or three litters after that succeeding the copulation with the mongrel. But the best instance of the kind was in the case of a mare belonging to Lord Morton, who, while he was in India, wished to obtain a

cross-breed between the horse and quagga, and caused this mare to be covered by a male quagga. The foal that she next bore had the distinct marks of the quagga, in the shape of its head, black bars on the legs and shoulders, and other characters. After this time she was thrice covered by horses, and every time the foal she bore had still distinct, though decreasing, marks of the quagga; the peculiar characters of the quagga being thus impressed not only on the ovum then impregnated, but on the three following ova impregnated by horses. It would appear, therefore, that the constitution of an impregnated female may become so altered and tainted with the peculiarities of the impregnating male, through the medium of the fœtus, that she necessarily imparts such peculiarities to any offspring she may subsequently bear by other males. Of the direct means by which a peculiarity of structure on the part of a male is thus transmitted, nothing whatever is known.

Development.

Changes in the Ovum up to formation of Blastoderm.

The earlier stages in development are so fundamentally similar in all vertebrate animals, from Fishes up to Man, that the gaps existing in our knowledge of the process in the higher Mammalia, such as man, may be in part, at any rate, filled up by the more accurate knowledge which we possess of the development of the ovum in such animals as the trout, frog, and fowl.

Before proceeding to describe these early stages, it will be necessary to point out one important distinction between the ova of various Vertebrata. In the hen's egg, besides the shell and the white or albumen, two other structures are to be distinguished—the *germ*, often called the cicatricula or "tread," and the *yelk* enclosed in its vitelline membrane.

The *germ* is essentially a cell, consisting of protoplasm enclosing a nucleus and nucleolus. It alone participates in the process of *segmentation* (to be immediately described), the great mass of the yelk (food-yelk) remaining quite unaffected by it. Since only the germ, which forms but a small portion of the yelk, undergoes segmentation, the ovum is called *meroblastic*.

In the Mammalia, on the other hand, there is no large unsegmented mass corresponding to the food-yelk of birds; the entire ovum undergoes segmentation, and is hence termed *holoblastic*.

The eggs of Fishes, Reptiles, and Birds, are meroblastic, while those of Amphibia and Mammalia are holoblastic.

Of the changes which the mammalian ovum undergoes previous to the formation of the embryo, some occur while it is still in the ovary, and are apparently independent of impregnation: others take place after it has reached the Fallopian tube. The knowledge we possess of these changes is derived almost exclusively from observations on the ova of the bitch and rabbit: but

it may be inferred that analogous changes ensue in the human ovum.

Bischoff describes the yelk of an ovarian ovum soon after coitus as being unchanged in its characters, with the single exception of being fuller and more dense; it is still granular, as before, and does not possess any of the cells subsequently found in it. The germinal vesicle always disappears, sometimes before the ovum leaves the ovary, at other times not until it has entered the Fallopian tube; but always before the commencement of the metamorphosis of the yelk.

Fig. 336.*

As the ovum approaches the middle of the Fallopian tube, it begins to receive a new investment, consisting of a layer of transparent albuminous or glutinous substance, which forms upon the exterior of the zona pellucida. It is at first exceedingly fine, and, owing to this, and to its transparency, is not easily recognised: but at the lower part of the Fallopian tube it acquires considerable thickness.

Segmentation.—The first visible result of fertilisation is a slight amœboid movement in the protoplasm of the ovum: this has been observed in some fish, in the frog, and in some mammals. Immediately succeeding to this the process of *segmentation* commences, and is completed during the passage of the ovum through the Fallopian tube. The whole yelk becomes constricted in the middle, and surrounded by a furrow which, gradually deepening, at length cuts the yelk in half, while the same process begins almost immediately in each half of the yelk, and cuts it also in two. The same process is repeated in each of the

* Fig. 336. Diagrams of the various stages of cleavage of the yelk Dalton).

quarters, and so on, until at last by continual cleavings the whole yelk is changed into a mulberry-like mass of small and more or less rounded bodies, sometimes called "vitelline spheres," the whole still enclosed by the *zona pellucida* or *vitelline membrane* (fig. 336). Each of these little spherules contains a transparent vesicle, like an oil-globule, which is seen with difficulty, on account of its being enveloped by the yelk-granules which adhere closely to its surface.

The cause of this singular subdivision of the yelk is quite obscure: though the immediate agent in its production seems to be the central vesicle contained in each division of the yelk. Originally there was probably but one vesicle, situated in the centre of the entire granular mass of the yelk, and probably derived from the germinal vesicle. This divides and subdivides: each successive division and subdivision of the vesicle being accompanied by a corresponding division of the yelk (see Reproduction by Fission, Chapter III.).

About the time at which the Mammalian ovum reaches the uterus, the process of division and subdivision of the yelk appears to have ceased, its substance having been resolved into its ultimate and smallest divisions, while its surface presents a uniform finely-granular aspect, instead of its late mulberry-like appearance. The ovum, indeed, appears at first sight to have lost all trace of the cleaving process, and, with the exception of being paler and more translucent, almost exactly resembles the ovarian ovum, its yelk consisting apparently of a confused mass of finely granular substance. But on a more careful examination, it is found that these granules are aggregated into numerous minute spheroidal masses, each of which contains a clear vesicle or nucleus in its centre, and is, in fact, an "embryonal cell." The zona pellucida, and the layer of albuminous matter surrounding it, have at this time the same character as when at the lower part of the Fallopian tube.

The passage of the ovum, from the ovary to the uterus, occupies probably eight or ten days in the human female.

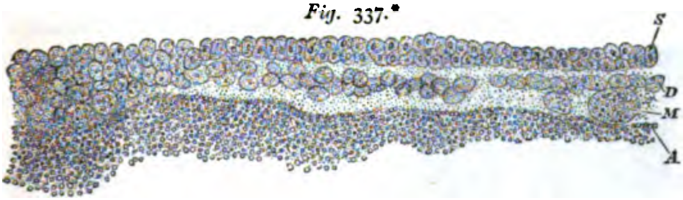
When the peripheral cells, which are formed first, are fully developed, they arrange themselves at the surface of the yelk into

a kind of membrane, and at the same time assume a polyhedral shape from mutual pressure, so as to resemble pavement epithelium. The deeper cells of the interior pass gradually to the surface and accumulate there, thus increasing the thickness of the membrane already formed by the more superficial layer of cells, while the central part of the yelk remains filled only with a clear fluid. By this means the yelk is shortly converted into a kind of secondary vesicle, the walls of which are composed externally of the original vitelline membrane, and within by the newly formed cellular layer, the *blastodermic* or *germinal* membrane, as it is called.

Before long the blastoderm is found to consist of three fundamental layers, *epiblast*, *mesoblast*, and *hypoblast*.

The way in which these are formed may be readily studied in a hen's egg,. In a freshly laid hen's egg, before incubation has commenced, the blastoderm is found to consist of two layers, (fig. 337, *S* and *D*) the upper of which forms a distinct membrane of columnar cells, while the lower stratum consists of larger cells irregularly arranged.

Fig. 337.*



Beneath the blastoderm are a few scattered larger cells—"formative cells." In the lower of the above two layers, some cells become flattened and unite to form a distinct membrane (hypoblast); the remaining cells of the lower layer, together with some of the large formative cells, which migrate by amœboid movement round the edge of the hypoblast, (Fig. 337, *M*), constitute a third layer (mesoblast).

* Fig. 337. Vertical section of *area pellucida*, and *area opaca* (left extremity of figure) of blastoderm of a fresh-laid egg (unincubated). *S*, superficial layer corresponding to epiblast; *D*, deeper layer, corresponding to hypoblast, and probably in part to mesoblast; *M*, large "formative cells," filled with yelk granules, and lying on the floor of the segmentation cavity; *A*, the white yelk immediately underlying the segmentation cavity (Stricker).

These important changes are among the earliest results of incubation.

Fig. 338.*

From the *epiblast* are ultimately developed the epidermis and its various appendages, also the cerebro-spinal *nerve centres*, the sensorial epithelium of the organs of special sense (eye, ear, nose), and the epithelium of the mouth and salivary glands.

From the *hypoblast* is developed the epithelium of the whole digestive canal together with that lining the ducts of all the glands which open into it; also the glandular parenchyma of the glands (*e.g.*, liver and pancreas) connected with it, and the epithelium of the respiratory tract.

From the *mesoblast* are derived all the tissues and organs of the body intervening between these two, the whole group of the connective tissues, the muscles and the cerebro-spinal and sympathetic *nerves*, with the vascular and genito-urinary systems, and all the digestive canal with its various appendages with the exception of the lining epithelium above mentioned.

First rudiments of the embryo and its chief organs.

Fig. 339.†

Germinal area.—The position in which the embryo is about to appear is early marked out by a central roundish opacity in the blastoderm, due to the accumulation of cells in this region. This *germinal area*, which is at first circular, changes its shape, becoming pyriform, and finally an elongated oval constricted in the middle like a savoy biscuit.

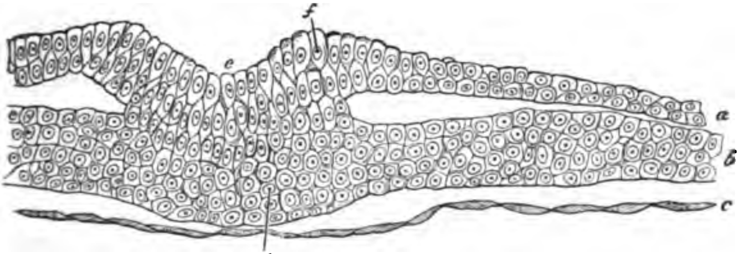
* Fig. 338. Vertical section of blastoderm of chick (1st day of incubation). *S*, epiblast, consisting of short columnar cells; *D*, hypoblast, consisting of a single layer of flattened cells; *M*, "formative cells." They are seen on the right of the figure, passing in between the epiblast and hypoblast to form the mesoblast; *A*, White yelk granules. Many of the large "formative cells" are seen containing these granules (Stricker).

† Fig. 339. Impregnated egg, with commencement of formation of embryo; showing the area germinativa or embryonic spot, the area pellucida, and the primitive groove or trace (Dalton).

The central portion becomes transparent, and thus we have an *area pellucida*, surrounded by an *area opaca* (fig. 339).

Primitive Groove.—The first trace of the embryo is a shallow longitudinal groove (*primitive groove*), which appears towards the posterior part of the area pellucida (figs. 339, 340).

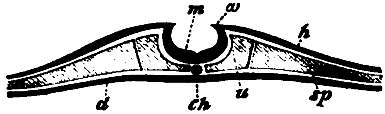
Fig. 340.*



Medullary Groove.—The primitive groove is but transitory, and is soon displaced by the *medullary groove*, which first appears at the anterior extremity of the future embryo, and grows backwards gradually causing the disappearance of the primitive groove.

Laminæ dorsales.—The medullary canal is bounded by two longitudinal elevations (*laminæ dorsales*) which are folds consisting entirely of cells of the epiblast: these grow up and arch over the medullary groove (fig. 341) till they coalesce in the middle line, converting it from an open furrow into a closed tube—the primitive cerebro-spinal axis. Over this closed tube, the walls of

Fig. 341.†



* Fig. 340. Transverse section through embryo chick (26 hrs.). *a*, epiblast; *b*, mesoblast; *c*, hypoblast; *d*, central portion of mesoblast, which is here fused with epiblast; *e*, primitive groove; *f*, dorsal ridge (Klein).

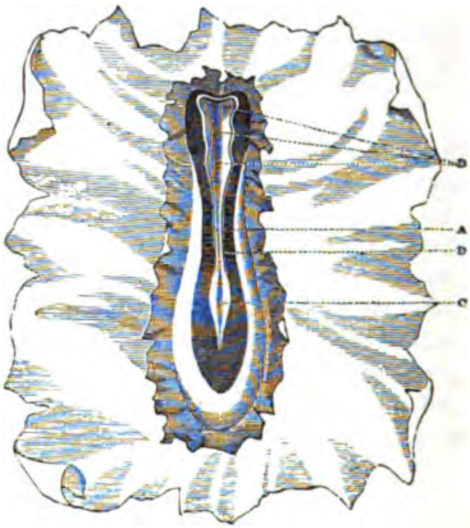
† Fig. 341. Diagram of transverse section through an embryo before the closing-in of the medullary groove. *m*, cells of epiblast lining the medullary groove which will form the spinal cord; *h*, epiblast; *d*, hypoblast; *ch*, notochord; *u*, protovertebra; *sp*, mesoblast; *w*, edge of lamina dorsalis, folding over medullary groove (Kölliker).

which consist of more or less cylindrical cells, the superficial layer of the epiblast is now continued as a distinct membrane.

The union of the medullary folds or laminæ dorsales takes place first about the neck of the future embryo; they soon after unite over the region of the head, while the closing in of the groove progresses much more slowly towards the hinder extremity of the embryo. The medullary groove is by no means of uniform diameter throughout, but even before the dorsal laminæ have united over it, is seen to be dilated at the anterior extremity and obscurely divided by constrictions into the three primary vesicles of the brain.

The part from which the spinal cord is formed is of nearly uniform calibre, while towards the posterior extremity is a lozenge-shaped dilatation, which is the last part to close in (fig. 342).

Fig. 342.*

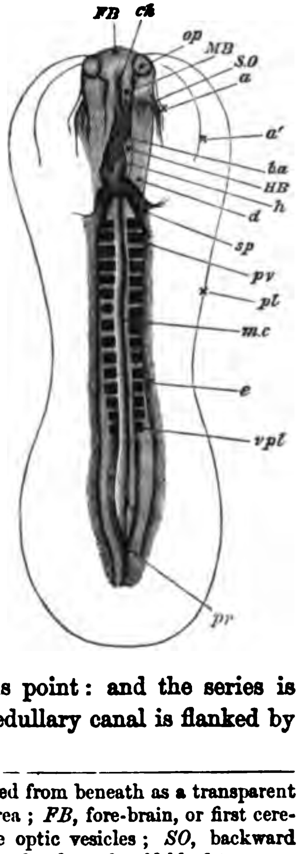


Notochord.—At the same time there appears in the middle line, immediately beneath the floor of the medullary groove, a

* Fig. 342. Portion of the germinal membrane, with rudiments of the embryo; from the ovum of a bitch. The primitive groove, A, is not yet closed, and at its upper or cephalic end presents three dilatations B, which correspond to the three divisions or vesicles of the brain. At its lower extremity the groove presents a lancet-shaped dilatation (sinus rhomboidalis) C. The margins of the groove consist of clear pellucid nerve-substance. Along the bottom of the groove is observed a faint streak, which is probably the chorda dorsalis. D. Vertebral plates (Bischoff).

rod-shaped structure formed by an aggregation of cells of the mesoblast; it soon becomes quite distinct from the remainder of the mesoblast, and constitutes an axial cord (notochord, *chorda dorsalis*) (*ch*, fig. 341) which extends nearly the whole length of the medullary canal, terminating anteriorly beneath the middle one of the three cerebral vesicles, and occupies the future position of the *bodies* of the vertebræ and basis cranii.

Fig. 343.*



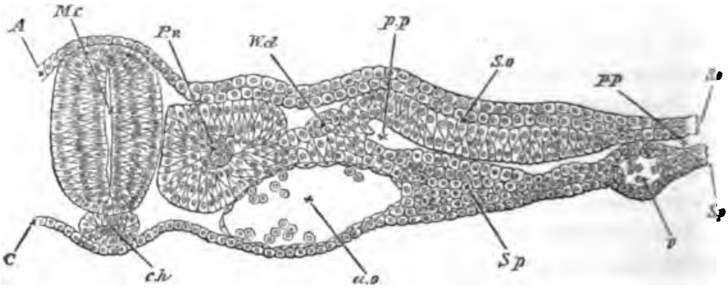
Protovertebræ. — Simultaneously on each side of the notochord appears a longitudinal thickening of the mesoblast.

Thus we have two lateral plates which when viewed from above are seen to be divided into a number of squarish segments (*protovertebræ*) by the formation of transverse clefts. The first three or four of these protovertebræ make their appearance in the cervical region, while one or two more are formed in front of this point: and the series is continued backward till the whole medullary canal is flanked by them (fig. 343).

* Fig. 343. Embryo chick (36 hrs.), viewed from beneath as a transparent object (magnified). *pl*, outline of pellucid area; *FB*, fore-brain, or first cerebral vesicle: from its sides project *op*, the optic vesicles; *SO*, backward limit of somatopleure fold, "tucked in" under head; *a*, headfold of true amnion; *a'*, reflected layer of amnion, sometimes termed "false amnion"; *sp*, backward limit of splanchnopleure folds, along which run the omphalomesaraic veins uniting to form *h*, the heart, which is continued forwards into *ba*, the bulbus arteriosus; *d*, the fore-gut, lying behind the heart, and having a wide crescentic opening between the splanchnopleure folds; *HB*, hindbrain; *MB*, mid-brain; *pv*, protovertebræ lying behind the fore-gut; *mc*, line of junction of medullary folds and of notochord; *ch*, front end of notochord; *vpl*, vertebral plates; *pr*, the primitive groove at its caudal end (Foster and Balfour).

Splitting of Mesoblast.—External to the protovertebræ, the mesoblast now splits into two laminæ (*parietal* and *visceral*): of these the former, when traced out from the central axis, is seen to be in close apposition with the epiblast and gives origin to the parietes of the trunk, while the latter adheres more or less closely to the hypoblast, and gives rise to the serous and muscular walls of the alimentary canal and several other parts (fig. 344).

Fig. 344.*



The united *parietal* layer of the mesoblast with the epiblast is termed *somatopleure*, the united *visceral* layer and hypoblast, *splanchnopleure*. The space between them is the pleuro-peritoneal cavity, which becomes subdivided by subsequent partitions into pericardium, pleura, and peritoneum.

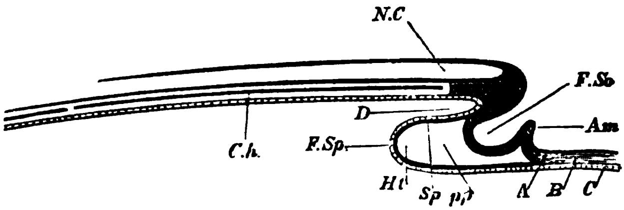
Head and tail folds. Body cavity.—Every vertebrate animal consists essentially of a longitudinal axis (vertebral column) with a neural canal above it, and a body-cavity (containing the alimentary canal) beneath.

We have seen how the earliest rudiments of the central axis and the neural canal are formed; we must now consider how the general body-cavity is developed. In its earliest stages the

* Fig. 344. Transverse section through dorsal region of embryo chick (45 hrs.). One half of the section is represented: if completed it would extend as far to the left as to the right of the line of the medullary canal (*Mc*). *A*, epiblast; *C*, hypoblast, consisting of a single layer of flattened cells; *Mc*, medullary canal; *Pv*, protovertebra; *Wd*, Wolffian duct; *So*, somatopleure; *Sp*, splanchnopleure; *pp*, pleuro-peritoneal cavity; *ch*, notochord; *ao*, dorsal aorta, containing blood cells; *v*, blood-vessels of the yolk-sac (Foster and Balfour).

embryo lies flat on the surface of the yelk, and is not clearly marked off from the rest of the blastoderm: but gradually a crescentic depression (with its concavity backwards) is formed in the blastoderm, limiting the head of the embryo; the blastoderm is, as it were, tucked in under the head, which thus comes to project above the general surface of the membrane: a similar tucking in of blastoderm takes place at the caudal extremity, and thus the head and tail folds are formed (fig. 345).

Fig. 345.*



Similar depressions mark off the embryo laterally, until it is completely surrounded by a sort of moat which it overhangs on all sides, and which clearly defines it from the yelk.

This moat runs in further and further all round beneath the overhanging embryo, till the latter comes to resemble a canoe turned upside-down, the ends and middle being, as it were, decked in by the folding or tucking in of the blastoderm, while on the ventral surface there is still a large communication with the yelk, corresponding to the "well" or undecked portion of the canoe.

This communication between the embryo and the yelk is gradually contracted by the further tucking in of the blastoderm from all sides, till it becomes narrowed down, as by an invisible

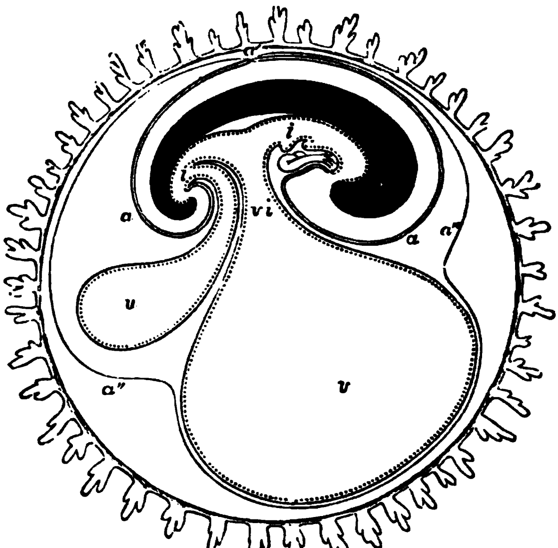
* Fig. 345. Diagrammatic longitudinal section through the axis of an embryo. The head-fold has commenced, but the tail-fold has not yet appeared. *FSo*, fold of the somatopleure; *FSp*, fold of the splanchnopleure; the line of reference, *FSo*, lies outside the embryo in the "moat," which marks off the overhanging head from the amnion; *D*, inside the embryo, is that part which is to become the fore-gut; *FSo* and *FSp*, are both parts of the head-fold, and travel to the left of the figure as development proceeds; *pp*, space between somatopleure and splanchnopleure, pleuro-peritoneal cavity; *Am*, commencing head-fold of amnion; *NC*, neural canal; *Ch*, notochord; *Ht*, heart; *A*, *B*, *C*, epiblast, mesoblast, hypoblast (Foster and Balfour).

constricting band, to a mere pedicle which passes out of the body of the embryo at the point of the future umbilicus.

The downwardly folded portions of blastoderm are termed the *visceral plates*.

Thus we see that the body-cavity is formed by the downward folding of the visceral plates, just as the neural cavity is produced by the upward growth of the dorsal laminæ, the difference

Fig. 346.*



* Fig. 346. Diagrammatic section showing the relation in a mammal between the primitive alimentary canal and the membranes of the ovum. The stage represented in this diagram corresponds to that of the fifteenth or seventeenth day in the human embryo, previous to the expansion of the allantois: *c*, the villous chorion; *a*, the amnion; *a′*, the place of convergence of the amnion and reflexion of the false amnion *a″ a″*, or outer or corneous layer; *e*, the head and trunk of the embryo, comprising the primitive vertebræ and cerebro-spinal axis; *i*, *i*, the simple alimentary canal in its upper and lower portions. Immediately beneath the right hand *i* is seen the fœtal heart, lying in the anterior part of the pleuro-peritoneal cavity; *v*, the yolk-sac, or umbilical vesicle; *v i*, the vitello-intestinal opening; *u*, the allantois connected by a pedicle with the anal portion of the alimentary canal (from Quain's "Anatomy)."

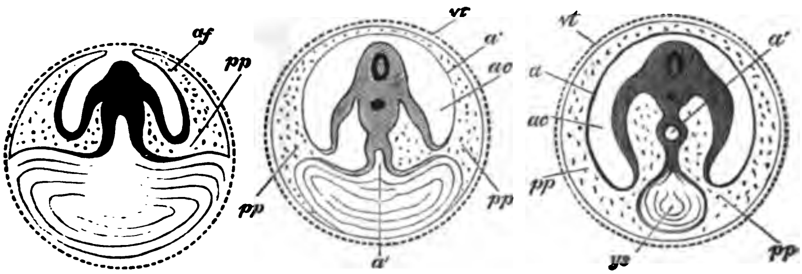
being that, in the visceral or ventral laminæ, all three layers of the blastoderm are concerned.

The folding in of the splanchnopleure, lined by hypoblast, pinches off, as it were, a portion of the yelk-sac, enclosing it in the body-cavity. This forms the rudiment of the alimentary canal, which at this period ends blindly towards the head and tail, while in the centre it communicates freely with the cavity of the yelk-sac through the canal termed *vitelline* or *omphalo-mesenteric duct*.

The yelk-sac thus becomes divided into two portions which communicate through the vitelline duct, that portion within the body giving rise, as above stated, to the digestive canal, and that outside the body remaining for some time as the *umbilical vesicle* (fig. 347, *ys*). The hypoblast forming the epithelium of the intestine is of course continuous with the lining membrane of the umbilical vesicle, while the visceral plate of the mesoblast is continuous with the outer layer of the umbilical vesicle.

All the above details will be clear on reference to the accompanying diagrams.

Fig. 347.*



* Fig. 347. Diagrams, showing three successive stages of development. Transverse vertical sections. The yelk-sac, *ys*, is seen progressively diminishing in size. In the embryo itself the medullary canal and notochord are seen in section. *a'*, in middle figure, the alimentary canal, becoming pinched off, as it were, from the yelk-sac; *a'* in right hand figure, alimentary canal completely closed; *a*, in last two figures, amnion; *ac*, cavity of amnion filled with amniotic fluid; *pp*, space between amnion and chorion, continuous with the pleuro-peritoneal cavity inside the body; *vt*, vitelline membrane; *ys*, yelk-sac, or umbilical vesicle (Foster and Balfour).

Fœtal Membranes.

Umbilical Vesicle or Yelk-sac.—The splanchnopleure, lined by hypoblast, forms the yelk-sac in Reptiles, Birds, and Mammals; but in Amphibia and Fishes, since there is neither *amnion* nor *allantois*, the wall of the yelk-sac consists of all three layers of the blastoderm, enclosed, of course, by the original vitelline membrane.

The body of the embryo becomes in great measure detached from the yelk-sac or umbilical vesicle, which contains, however, the greater part of the substance of the yelk, and furnishes a source whence nutriment is derived for the embryo. This nutriment is absorbed by the numerous vessels (omphalo-mesenteric) which ramify in the walls of the yelk-sac, forming what in birds is termed the *area vasculosa*. In birds, the contents of the yelk-sac afford nourishment until the end of incubation, and the omphalo-mesenteric vessels are developed to a corresponding degree; but in Mammalia the office of the umbilical vesicle

Fig. 348.*

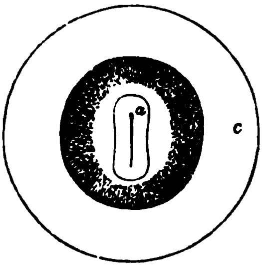
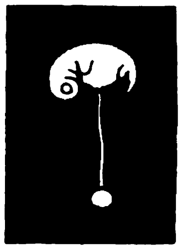


Fig. 349.†



ceases at a very early period, the quantity of yelk is small, and the embryo soon becomes independent of it by the connections it forms with the parent. Moreover, in Birds, as the sac is emptied, it is gradually drawn into the abdomen through the

* Fig. 348. Diagram showing vascular area in the chick. *a*, area pellucida; *b*, area vasculosa; *c*, area vitellina.

† Fig. 349. Human embryo of fifth week with umbilical vesicle; about natural size (Dalton). The human umbilical vesicle never exceeds the size of a small pea.

umbilical opening, which then closes over it: but in Mammalia it always remains on the outside; and as it is emptied it contracts (fig. 349), shrivels up, and together with the part of its duct external to the abdomen, is detached and disappears either before or at the termination of intra-uterine life, the period of its disappearance varying in different orders of Mammalia.

When blood-vessels begin to be developed, they ramify largely over the walls of the umbilical vesicle, and are actively concerned in absorbing its contents and conveying them away for the nutrition of the embryo.

The Amnion and Allantois.—At an early stage of development of the fœtus, and some time before the completion of the changes which have been just described, two important structures, called respectively the *amnion* and the *allantois*, begin to be formed.

Amnion.—The amnion is produced as follows:—Beyond the head- and tail-folds before described (p. 750), the somatopleure, coated by epiblast, is raised into folds, which grow up, arching over the embryo, not only anteriorly and posteriorly but also laterally, and all converging towards one point over its dorsal surface (fig. 350). The growing up of these folds from all sides and their convergence towards one point very closely resembles the folding inwards of the visceral plates already described, and hence, by some, the point at which the amniotic folds meet over the back has been termed the "amniotic umbilicus."

Fig. 350.*

The folds not only come into contact but coalesce. The inner of the two layers forms the *true amnion*, while the outer or reflected layer, sometimes termed the *false amnion*, coalesces with the inner surface of the original vitelline membrane to form the

* Fig. 350. Diagram of fecundated egg. *a*, umbilical vesicle; *b*, amniotic cavity; *c*, allantois (Dalton.)

chorion. This growth of the amniotic folds must of course be clearly distinguished from the very similar process, already described, by which the walls of the neural canal are formed at a much earlier stage.

The cavity between the true amnion and the external surface of the embryo becomes a closed space, termed the *amniotic cavity* (*ac*, fig. 347).

At first, the amnion closely invests the embryo, but it becomes gradually distended with fluid (liquor amnii), which, as pregnancy advances, reaches a considerable quantity.

This fluid consists of water containing small quantities of albumen and urea. Its chief function during gestation appears to be the mechanical one of affording equal support to the embryo on all sides, and of protecting it as far as possible from the effects of blows and other injuries to the abdomen of the mother.

The embryo up to the end of pregnancy is thus immersed in fluid, which during parturition serves the important purpose of gradually and evenly dilating the neck of the uterus to allow of the passage of the fœtus : when this is accomplished the amniotic sac bursts and the "waters" escape.

On referring to the diagrams (fig. 347), it will be obvious that the cavity outside the amnion (between it and the false amnion) is continuous with the pleuro-peritoneal cavity at the umbilicus.

Fig. 351.*

This cavity is not entirely obliterated even at birth, and contains a small quantity of fluid ("false waters"), which is discharged during parturition either before, or at the same time as the amniotic fluid.

Allantois.—Into the pleuro-peritoneal space the *allantois* sprouts out, its formation commencing during the development of the amnion.

Growing out from or near the hinder portion of the intestinal

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* Fig. 351. Fecundated egg with allantois nearly complete. *a*, inner layer of amniotic fold ; *b*, outer layer of ditto ; *c*, point where the amniotic folds come in contact. The allantois is seen penetrating between the outer and inner layers of the amniotic folds. This figure, which represents only the amniotic folds and the parts within them, should be compared with figs. 347, 353, in which will be found the structures external to these folds (Dalton).

canal (*c*, fig. 350), with which it communicates, the allantois is at first a solid pear-shaped mass of splanchnopleure; but becoming vesicular by the projection into it of a hollow out-growth of hypoblast, and very soon simply membranous and vascular, it insinuates itself between the amniotic folds, just described, and comes into close contact and union with the outer of the two folds, which has itself, as before said, become one with the external investing membrane of the egg. As it grows, the allantois developes muscular tissue in its external wall and becomes exceedingly vascular; in birds (fig. 351) it envelopes the whole embryo—taking up vessels, so to speak, to the outer investing membrane of the egg, and lining the inner surface of the shell with a vascular membrane, by these means affording an extensive surface in which the blood may be aerated. In the human subject and in other Mammalia, the vessels carried out by the allantois are distributed only to a special part of the outer membrane or *chorion*, where, by interlacement with the vascular system of the mother, a structure called the *placenta* is developed.

In Mammalia, as the visceral laminæ close in the abdominal cavity, the allantois is thereby divided at the umbilicus into two portions; the outer part, extending from the umbilicus to the *chorion*, soon shrivelling; while the inner part, remaining in the abdomen, is in part converted into the urinary bladder; the portion of the inner part not so converted, extending from the bladder to the umbilicus, under the name of the *urachus*. After birth the umbilical cord, and with it the external and shrivelled portion of the allantois, are cast off at the umbilicus, while the *urachus* remains as an impervious cord stretched from the top of the urinary bladder to the umbilicus, in the middle line of the body, immediately beneath the parietal layer of the peritoneum. It is sometimes enumerated among the ligaments of the bladder.

It must not be supposed that the phenomena which have been successively described, occur in any regular order one after another. On the contrary, the development of one part is going on side by side with that of another.

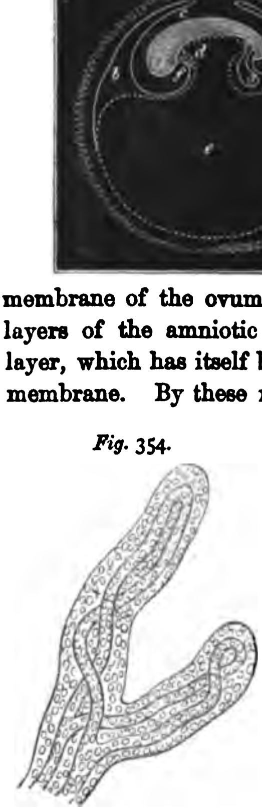
The Chorion.

It has been already remarked that the *allantois* is a structure which extends from the body of the fœtus to the outer investing

Fig. 352. *Fig.* 353.*

membrane of the ovum, that it insinuates itself between the two layers of the amniotic fold, and becomes fused with the outer layer, which has itself become previously fused with the vitelline membrane. By these means the external investing membrane of the ovum, or the *chorion*, as it is now called, represents three layers, namely, the original vitelline membrane, the outer layer of the amniotic fold, and the allantois.

Fig. 354.



Very soon after the entrance of the ovum into the uterus, in the human subject, the outer surface of the chorion is found beset with fine processes, the so-called *villi of the chorion* (*a*, figs. 352, 353), which give it a rough and shaggy appearance. At first only cellular in structure, these little outgrowths subsequently become vascular by the development in them of loops of

* Figs. 352 and 353 (after Todd and Bowman). *a*, chorion with villi. The villi are shown to be best developed in the part of the chorion to which the allantois is extending; this portion ultimately becomes the placenta; *b*, space between the two layers of the amnion; *c*, amniotic cavity; *d*, situation of the intestine, showing its connection with the umbilical vesicle; *e*, umbilical vesicle; *f*, situation of heart and vessels; *g*, allantois.

capillaries (fig. 354); and the latter at length form the minute extremities of the blood-vessels which are, so to speak, conducted from the fœtus to the chorion by the allantois. The function of the villi of the chorion is evidently the absorption of nutrient matter for the fœtus; and this is probably supplied to them at first from the fluid matter, secreted by the follicular glands of the uterus, in which they are soaked. Soon, however, the fœtal vessels of the villi come into more intimate relation with the vessels of the uterus. The part at which this relation between the vessels of the fœtus and those of the parent ensues, is not, however, over the whole surface of the chorion: for, although all the villi become vascular, yet they become indistinct or disappear except at one part where they are greatly developed, and by their branching give rise, with the vessels of the uterus, to the formation of the *placenta*.

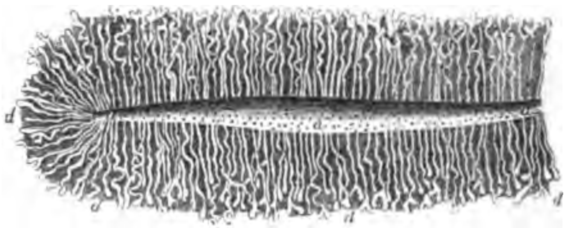
To understand the manner in which the *fœtal* and *maternal* blood-vessels come into relation with each other in the placenta, it is necessary briefly to notice the changes which the uterus undergoes after impregnation. These changes consist especially of alterations in structure of the superficial part of the mucous membrane which lines the interior of the uterus, and which forms, after a kind of development to be immediately described, the *membrana decidua*, so called on account of its being discharged from the uterus at birth.

Changes of the Mucous Membrane of the Uterus, and Formation of the Placenta.

The mucous membrane of the human uterus, which consists of a matrix of connective tissue containing numerous corpuscles (adenoid tissue), and is lined internally by columnar ciliated epithelium, is abundantly beset with tubular glands, arranged perpendicularly to the surface (fig. 355). These follicles are very small in the unimpregnated uterus; but when examined shortly after impregnation, they are found elongated, enlarged, and much waved and contorted towards their deep and closed extremity, which is implanted at some depth in the tissue of the uterus, and may dilate into two or three closed sacculi (fig. 355).

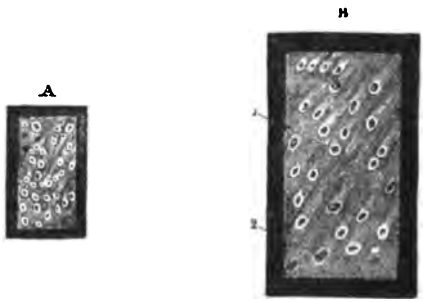
The glands are lined by columnar ciliated epithelium (p. 722), and they open on the inner surface of the mucous membrane by small round orifices set closely together (*a*, *a*, fig. 355).

Fig. 355.*



On the internal surface of the mucous membrane may be seen the circular orifices of the glands, many of which are, in the early period of pregnancy, surrounded by a whitish ring, formed of the epithelium which lines the follicles (fig. 356).

Fig. 356.†



* Fig. 355. Section of the lining membrane of a human uterus at the period of commencing pregnancy, showing the arrangement and other peculiarities of the glands, *d*, *d*, *d*, with their orifices, *a*, *a*, *a*, on the internal surface of the organ. Twice the natural size.

† Fig. 356. Two thin segments of human decidua after recent impregnation, viewed on a dark ground: they show the openings on the surface of the membrane. A is magnified six diameters, and B twelve diameters. At 1, the lining of epithelium is seen within the orifices, at 2 it has escaped (Sharpey).

Coincidently with the occurrence of pregnancy, important changes occur in the structure of the mucous membrane of the uterus. The epithelium and sub-epithelial connective tissue, together with the tubular glands, increase rapidly, and there is a greatly increased vascularity of the whole mucous membrane, the vessels of the mucous membrane becoming larger and more numerous; while a substance composed chiefly of nucleated cells fills up the interfollicular spaces in which the blood-vessels are contained. The effect of these changes is an increased thickness, softness, and vascularity of the mucous membrane, the superficial part of which itself forms the *membrana decidua.*

The object of this increased development seems to be the production of nutritive materials for the ovum; for the cavity of the uterus shortly becomes filled with secreted fluid, consisting almost entirely of nucleated cells, in which the villi of the chorion are imbedded.

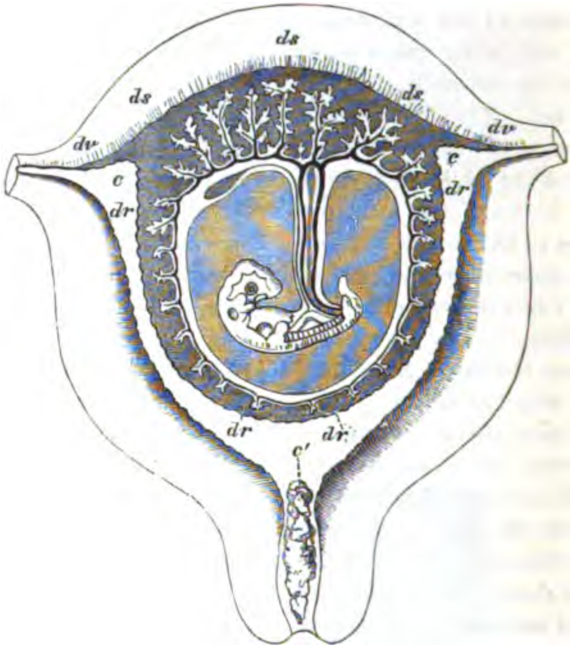
When the ovum first enters the uterus it becomes imbedded in the structure of the decidua, which is yet quite soft, and in which soon afterwards three portions are distinguishable. These have been named the decidua *vera,* the decidua *reflexa,* and the decidua *serotina.* The first of these, the decidua *vera,* lines the cavity of the uterus; the second, or decidua *reflexa,* is a part of the decidua vera, which grows up around the ovum, and, wrapping it closely, forms its immediate investment. The third, or decidua *serotina,* is the part of the decidua vera which becomes especially developed in connection with those villi of the chorion which, instead of disappearing, remain to form the fœtal part of the *placenta.*

In connection with these villous *processes* of the chorion, there are developed *depressions* or *crypts* in the decidual mucous membrane, which correspond in shape with the villi they are to lodge; and thus the chorionic villi become more or less imbedded in the maternal structures. These uterine crypts, it is important to note, are not, as was once supposed, merely the open mouths of the uterine follicles (Turner).

As the ovum increases in size, the decidua vera and the decidua reflexa gradually come into contact, and in the third

month of pregnancy the cavity between them has quite disappeared. Henceforth it is very difficult, or even impossible, to distinguish the two layers.

Fig. 357.*



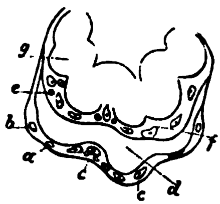
During these changes the deeper part of the mucous membrane of the uterus, at and near the region where the placenta is

* Fig. 357. Diagrammatic view of a transverse section of the uterus at the seventh or eighth week of pregnancy. *c, c, c'*, cavity of uterus, which becomes the cavity of the decidua, opening at *c, c*, the cornua, into the Fallopian tubes, and at *c'* into the cavity of the cervix, which is closed by a plug of mucus; *d v*, decidua vera; *d r*, decidua reflexa, with the sparser villi imbedded in its substance; *d s*, decidua serotina, involving the more developed chorionic villi of the commencing placenta. The fœtus is seen lying in the amniotic sac; passing up from the umbilicus is seen the umbilical cord and its vessels, passing to their distribution in the villi of the chorion; also the pedicle of the yelk sac, which lies in the cavity between the amnion and chorion (Allen Thomson).

placed, becomes hollowed out by sinuses, or cavernous spaces, which communicate on the one hand with arteries and on the other with veins of the uterus. Into these sinuses the villi of the chorion protrude, pushing the thin wall of the sinus before them, and so come into intimate relation with the blood contained in them. There is no direct communication between the blood-vessels of the mother and those of the fœtus; but the layer or layers of membrane intervening between the blood of the one and of the other offer no obstacle to a free interchange of matters between them. Thus the villi of the chorion, containing fœtal blood, are bathed or soaked in maternal blood contained in the uterine sinuses. The arrangement may be roughly compared to filling a glove with fœtal blood, and dipping its fingers into a vessel containing maternal blood. But in the fœtal villi there is a constant stream of blood into and out of the loop of capillary blood-vessel contained in it, as there is also into and out of the maternal sinuses.

It would seem from the observations of Professor Goodsir, that, at the villi of the placental tufts, where the fœtal and maternal portions of the placenta are brought into close relation with each other, the blood in the vessels of the mother is separated from that in the vessels of the fœtus by the intervention of two distinct sets of nucleated cells (fig. 358). One of these (*b*) belongs to the maternal portion of the placenta, is placed between the membrane of the villus and that of the vascular system of the mother, and is probably designed to separate from the blood of the parent the materials destined for the blood of the fœtus; the other (*f*) belongs to the fœtal portion of the placenta, is situated between the membrane of the villus and the loop of vessels contained within, and pro-

Fig. 358.*



* Fig. 358. Extremity of a placental villus. *a*, lining membrane of the vascular system of the mother; *b*, cells immediately lining *a*; *d*, space between the maternal and fœtal portions of the villus; *e*, internal membrane of the villus, or external membrane of the chorion; *f*, internal cells of the villus, or cells of the chorion; *g*, loop of umbilical vessels (Goodsir).

bably serves for the absorption of the material secreted by the other sets of cells, and for its conveyance into the blood-vessels of the fœtus. Between the two sets of cells with their investing membrane there exists a space (*d*), into which it is probable that the materials secreted by the one set of cells of the villus are poured in order that they may be absorbed by the other set, and thus conveyed into the fœtal vessels.

Not only, however, is there a passage of materials from the blood of the mother into that of the fœtus, but there is a mutual interchange of materials between the blood both of fœtus and of parent; the latter supplying the former with nutriment, and in turn abstracting from it materials which require to be removed.

Dr. Alexander Harvey's experiments were very decisive on this point. The view has also received abundant support from Mr. Hutchinson's important observations on the communication of syphilis from the father to the mother, through the instrumentality of the fœtus; and still more from Mr. Savory's experimental researches, which prove quite clearly that the female parent may be directly inoculated through the fœtus. Having opened the abdomen and uterus of a pregnant bitch, Mr. Savory injected a solution of strychnia into the abdominal cavity of one fœtus, and into the thoracic cavity of another, and then replaced all the parts, every precaution being taken to prevent escape of the poison. In less than half an hour, the bitch died from tetanic spasms; the fœtuses operated on were also found dead, while the others were alive and active. The experiments, repeated on other animals with like results, leave no doubt of the rapid and direct transmission of matter from the fœtus to the mother, through the blood of the placenta.

The placenta, therefore, of the human subject is composed of a *fœtal* part and a *maternal* part,—the term placenta properly including all that entanglement of fœtal villi and maternal sinuses, by means of which the blood of the fœtus is enriched and purified after the fashion necessary for the proper growth and development of those parts which it is destined to nourish.

The whole of this structure is not, as might be imagined, thrown off immediately after birth. The greater part, indeed, comes away at that time, as the *after-birth*; and the separation of this portion takes place by a rending or crushing through of that part at which its cohesion is least strong, namely, where it is most burrowed and undermined by the cavernous spaces before referred to. In this way it is cast off with the fœtal membrane

and the decidua *vera* and *reflexa*, together with a part of the decidua *serotina*. The remaining portion withers, and disappears by being gradually either absorbed, or thrown off in the uterine discharges or the *lochia*, which occur at this period.

A new mucous membrane is of course gradually developed, as the old one, by its peculiar transformation into what is called the decidua, ceases to perform its original functions.

The *umbilical cord*, which in the latter part of fœtal life is almost solely composed of the two arteries and the single vein which respectively convey fœtal blood to and from the placenta, contains the remnants of other structures which in the early stages of the development of the embryo were, as already related, of great comparative importance. Thus, in early fœtal life, it is composed of the following parts:—(1). Externally, a layer of the amnion, reflected over it from the umbilicus. (2). The umbilical vesicle with its duct and appertaining omphalo-mesenteric blood-vessels. (3). The remains of the allantois, and continuous with it the urachus. (4). The umbilical vessels, which, as just remarked, ultimately form the greater part of the cord.

DEVELOPMENT OF ORGANS.

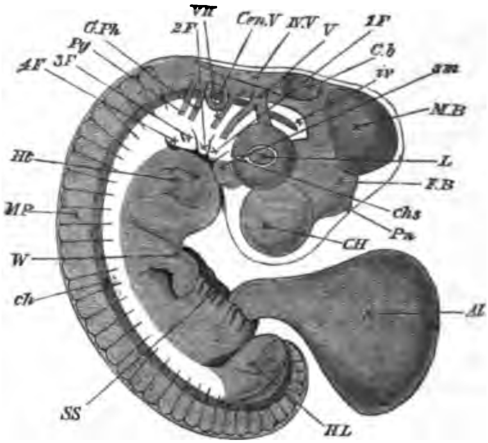
It remains now to consider in succession the development of the several organs and systems of organs in the further progress of the embryo. The accompanying figure (fig. 359) shows the chief organs of the body in a moderately early stage of development.

Development of the Vertebral Column and Cranium.

The primitive part of the vertebral column in all the Vertebrata is the *chorda dorsalis* (notochord), which consists entirely of soft cellular cartilage. This cord tapers to a point at the cranial and caudal extremities of the animal. In the progress of its development, it is found to become enclosed in a membranous sheath, which at length acquires a fibrous structure, composed of transverse annular fibres. The chorda dorsalis is to be regarded as the azygos axis of the spinal column, and, in particular, of the future bodies of the vertebræ, although it never itself passes into the state of hyaline cartilage or bone, but remains enclosed as

in a case within the persistent parts of the vertebral column which are developed around it. It is permanent, however, only in a few animals: in the majority only traces of it persist in the adult animal.

Fig. 359.*



In many Fish no true vertebræ are developed, and there is every gradation from the *amphioxus*, in which the notochord persists through life and there are no vertebral segments, through the lampreys in which there are a few scattered car-

* Fig. 359. Embryo chick (4th day), viewed as a transparent object, lying on its left side (magnified). *C H*, cerebral hemispheres; *F B*, fore-brain or vesicle of third ventricle, with *P n*, pineal gland projecting from its summit; *M B*, mid-brain; *C b*, cerebellum; *IV. V*, fourth ventricle; *L*, lens; *c h s*, choroidal slit; *Cen V*, auditory vesicle; *s m*, superior maxillary process; 1 *F*, 2 *F*, &c., first, second, third, and fourth visceral folds; *V*, fifth nerve, sending one branch (ophthalmic) to the eye, and another to the first visceral arch; *VII*, seventh nerve, passing to the second visceral arch; *G Ph*, glosso-pharyngeal nerve, passing to the third visceral arch; *P g*, pneumogastric nerve, passing towards the fourth visceral arch; *i v*, investing mass; *ch*, notochord; its front end cannot be seen in the living embryo, and it does not end as shown in the figure, but takes a sudden bend downwards, and then terminates in a point; *H t*, heart seen through the walls of the chest; *M P*, muscle-plates; *W*, wing, showing commencing differentiation of segments, corresponding to arm, forearm, and hand; *H L*, hind-limb, as yet a shapeless bud, showing no differentiation. Beneath it is seen the curved tail (Foster & Balfour).

tilaginous segments, and the sharks, in which many of the vertebræ are partly ossified, to the bony fishes, such as the cod and herring, in which the vertebral column consists of a number of distinct ossified vertebræ, with remnants of the notochord between them. In Amphibia, Reptiles, Birds, and Mammals, there are distinct vertebræ, which are formed as follows:—

The *protovertebræ*, which have been already mentioned (p. 749), send processes downwards and inwards to surround the notochord, and also upwards between the medullary canal and the epiblast covering it. In the former situation, the cartilaginous bodies of the vertebræ make their appearance, in the latter their arches, which enclose the neural canal.

The vertebræ do not exactly correspond in their position with the protovertebræ: but each permanent vertebra is developed from the contiguous halves of two protovertebræ. The original segmentation of the protovertebræ disappears, and a fresh subdivision occurs in such a way that a permanent intervertebral disc is developed opposite the centre of each protovertebra. Meanwhile the protovertebræ split into a dorsal and ventral portion. The former is termed the *musculo-cutaneous* plate, and from it are developed all the muscles of the back together with the cutis of the dorsal region (the epidermis being derived from the epiblast). The ventral portions of the protovertebræ, as we have already seen, give rise to the vertebræ and heads of the ribs, but the outer part of each also gives rise to a spinal ganglion and nerve-root.

The chorda is now enclosed in a case, formed by the bodies of the vertebræ, but it gradually wastes and disappears. Before the disappearance of the chorda, the ossification of the bodies and arches of the vertebræ begins at distinct points.

The ossification of the body of a vertebra is first observed at the point where the two primitive elements of the vertebræ have united inferiorly. Those vertebræ which do not bear ribs, such as the cervical vertebræ, have generally an additional centre of ossification in the transverse process, which is to be regarded as an abortive rudiment of a rib. In the fœtal bird, these additional ossified portions exist in all the cervical vertebræ, and gradually

become so much developed in the lower part of the cervical region as to form the upper false ribs of this class of animals. The same parts exist in mammalia and man; those of the last cervical vertebræ are the most developed, and in children may, for a considerable period, be distinguished as a separate part on each side, like the root or head of a rib.

The true cranium is a prolongation of the vertebral column, and is developed at a much earlier period than the facial bones. Originally, it is formed of but one mass, a cerebral capsule, the chorda dorsalis being continued into its base, and ending there with a tapering point. At an early period the head is bent downwards and forwards round the end of the chorda dorsalis in such a way that the *middle* cerebral vesicle, and not the anterior, comes to occupy the highest position in the head.

Pituitary Body.—In connection with this must be mentioned the development of the pituitary body. It is formed by the meeting of two out-growths, one from the fœtal brain, which grows downwards, and the other from the epiblast of the buccal cavity, which grows up towards it. The surrounding mesoblast also takes part in its formation. The connection of the first process with the brain becomes narrowed, and persists as the infundibulum, while that of the other process with the buccal cavity disappears completely at a spot corresponding with the future position of the body of the sphenoid.

The first appearance of a solid support at the base of the cranium observed by Müller in fish, consists of two elongated bands of cartilage (trabeculæ cranii), one on the right and the other on the left side, which are connected with the cartilaginous capsule of the auditory apparatus, and which diverge to enclose the pituitary body, uniting in front to form the septum nasi beneath the anterior end of the cerebral capsule. Hence, in the cranium, as in the spinal column, there are at first developed at the sides of the chorda dorsalis two symmetrical elements, which subsequently coalesce, and may wholly enclose the chorda.

The brain-case consists of three segments: occipital, parietal, and frontal, corresponding in their relative position to the three primitive cerebral vesicles; it may also be noted that in front of

each segment is developed a sense-organ (auditory, ocular, and olfactory, from behind forwards). The basis cranii consists at an early period of an unsegmented cartilaginous rod, developed round the notochord, and continued forward beyond its termination into the *trabeculæ cranii*, which bound the pituitary fossa on either side.

In this cartilaginous rod three centres of ossification appear: basi-occipital, basi-sphenoid, and pre-sphenoid, one corresponding to each segment.

The bones forming the vault of the skull (frontal, parietal, squamous portion of temporal), with the exception of the squamo-occipital, which is preformed in cartilage, are ossified in membrane.

Development of the Face and Visceral Arches.

It has been said before that at an early period of development of the embryo, there grow up on the sides of the primitive groove the so-called *dorsal laminæ*, which at length coalesce, and complete by their union the spinal canal. The same process essentially takes place in the head, so as to enclose the cranial cavity.

The so-called *visceral laminæ* have been also described as passing forwards, and gradually coalescing in front, as the dorsal laminæ do behind, and thus enclosing the thoracic and abdominal cavity. An analogous process occurs in the facial and cervical regions, but the enclosing laminæ, instead of being simple, as in the former instances, are cleft.

In this way the so-called visceral *arches* and *clefts* are formed, four on each side (fig. 360, A).

From or in connection with these arches the following parts are developed :—

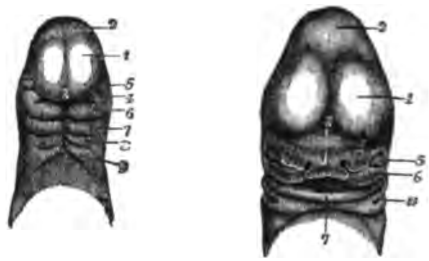
The first arch (mandibular) contains a cartilaginous rod (Meckel's cartilage), around the distal end of which the lower jaw is developed, while the malleus is ossified from the proximal end.

From near the root of this arch the maxillary process grows forwards and inwards towards the middle line; from it are formed the superior maxillary and malar bones. A pair of cartilaginous rods (pterygo-palatine), parallel to the trabeculæ cranii, give origin to the external pterygoid plate of the sphenoid and the palate bones.

The cleft between the maxillary process and the mandibular (or first visceral arch) forms the mouth.

When the maxillary processes on the two sides fail partially or completely to unite in the middle line, the well-known condition termed *cleft palate* results. When the integument of the face presents a similar deficiency,

Fig. 360.*



we have the deformity known as *hare-lip.* Though these two deformities frequently co-exist, they are by no means always necessarily associated.

The upper part of the face in the middle line is developed from the so-called *fronto-nasal* process (A, 3, fig. 360). From the *second* arch are developed the *incus*, *stapes*, the *stapedius* muscle, the styloid process of the *temporal* bone, the *stylo-hyoid* ligament, and the *smaller cornu* of the *hyoid* bone. From the *third* visceral arch, the *greater cornu* and *body* of the hyoid bone. In man and other mammalia the *fourth* visceral arch is indistinct. It occupies the position where the neck is afterwards developed.

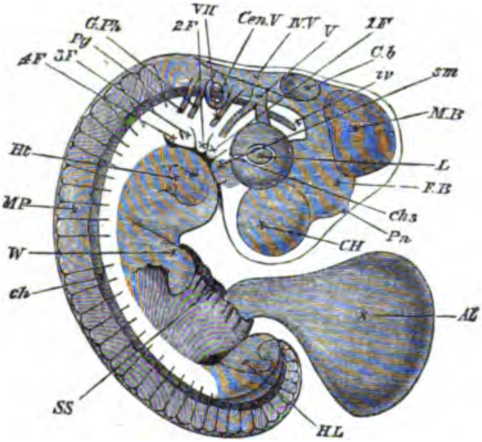
A distinct connection is traceable between these visceral arches and certain cranial nerves: the trigeminal, the facial, the glosso-pharyngeal, and the pneumogastric. The ophthalmic division of the trigeminal supplies the trabecular arch; the superior and inferior maxillary divisions supply the maxillary and mandibular arches respectively.

The facial nerve distributes one branch (chorda tympani) to the first visceral arch, and others to the second visceral arch. Thus it divides, enclosing the first visceral cleft.

* Fig. 360. A. Magnified view from before of the head and neck of a human embryo of about three weeks (from Ecker).—1, anterior cerebral vesicle or cerebrum; 2, middle ditto; 3, middle or fronto-nasal process; 4, superior maxillary process; 5, eye; 6, inferior maxillary process, or first visceral arch, and below it the first cleft; 7, 8, 9, second, third, and fourth arches and clefts. B. Anterior view of the head of a human fœtus of about the fifth week (from Ecker, as before, fig. IV.). 1, 2, 3, 5, the same parts as in A; 4, the external nasal or lateral frontal process; 6, the superior maxillary process; 7, the lower jaw; +, the tongue; 8, first branchial cleft becoming the meatus auditorius externus.

Similarly, the glosso-pharyngeal divides to enclose the second visceral cleft, its lingual branch being distributed to the second, and its pharyngeal branch to the third arch.

Fig. 361.*



The vagus, too, sends a branch (pharyngeal) along the third arch, and in fishes it gives off paired branches, which divide to enclose several successive branchial clefts.

Development of the Extremities.

The Extremities are developed in an uniform manner in all vertebrate animals. They appear in the form of leaf-like elevations from the parieties of the trunk (see fig. 362), at points where more or less of an arch will be produced for them within. The primitive form of the extremity is nearly the same in all Vertebrata, whether it be destined for swimming, crawling, walking, or flying. In the human fœtus the fingers are at first united, as if webbed for swimming; but this is to be regarded not so much as an approximation to the form of aquatic animals, as the primitive form of the hand, the individual parts of which subsequently become more completely isolated.

* For description see fig. 359.

The fore-limb always appears before the hind-limb and for some time continues in a more advanced state of development.

Fig. 362.*

In both limbs alike, the distal segment (hand or foot) is separated by a slight notch from the proximal part of the limb, and this part is subsequently divided again by a second notch (knee or elbow-joint).

Development of the Vascular System.

Histology.—At an early stage in the development of the embryo-chick, the so-called "area vasculosa" begins to make its appearance. A number of branched cells in the mesoblast send out processes which unite so as to form a network of protoplasm with nuclei at the nodal points. A large number of the nuclei acquire a red colour; these form the red blood-cells. The protoplasmic processes become hollowed out in the centre so as to form a closed system of branching canals, in

* Fig. 362. A human embryo of the fourth week, 3½ lines in length. 1, the chorion; 3, part of the amnion; 4, umbilical vesicle with its long pedicle passing into the abdomen; 7, the heart; 8, the liver; 9, the visceral arch destined to form the lower jaw, beneath which are two other visceral arches separated by the branchial clefts; 10, rudiment of the upper extremity; 11, that of the lower extremity; 12, the umbilical cord; 15, the eye; 16, the ear; 17, cerebral hemispheres; 18, optic lobes, corpora quadrigemina (Müller).

the walls of which the rest of the nuclei remain imbedded. In the blood-vessels thus formed, the circulation of the embryonic blood commences.

According to Dr. Klein's researches, the first blood-vessels in the chick are developed from embryonic cells of the mesoblast, which swell up and become vacuolated, while their nuclei undergo segmentation. These cells send out protoplasmic processes, which unite with corresponding ones from other cells, and become hollowed, giving rise to the capillary wall composed of endothelial cells; the blood corpuscles being budded off from the endothelial wall by a process of gemmation.

Heart.—About the same time the heart makes its appearance as a solid mass of cells of the splanchno-pleure.

At this period the anterior part of the alimentary tube ends blindly beneath the notochord. It is beneath the posterior end of this "fore-gut" (as it may be termed) that the heart begins to be developed. A cavity is hollowed out longitudinally in the mass of cells; the central cells float freely in the fluid, which soon begins to circulate by means of the rhythmic pulsations of the embryonic heart.

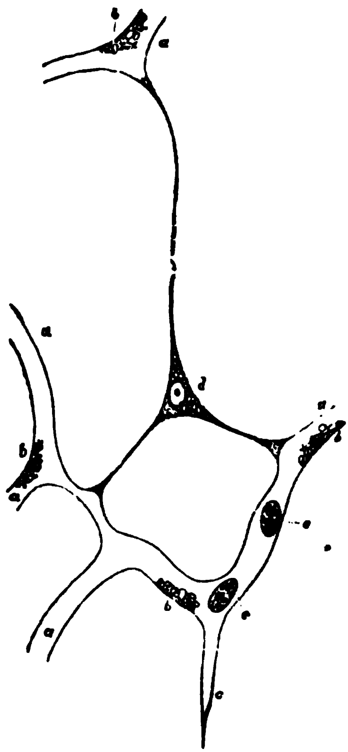
These pulsations take place even before the appearance of a cavity, and immediately after the first "laying down" of the cells from which the heart is formed, and long before muscular fibres or ganglia have been formed in the cardiac walls. At first they seldom exceed from fifteen to eighteen in the minute. The fluid within the cavity of the heart shortly assumes the characters of blood. At the same time the cavity itself forms a communication with the great vessels in contact with it, and the cells of which its walls are composed are transformed into fibrous and muscular tissues, and into epithelium. In the developing chick it can be observed with the naked eye as a minute red pulsating point before the end of the second day of incubation. Harvey, who discovered the circulation of the blood, was the first to describe it under the name of "punctum saliens."

Blood-vessels.—Blood-vessels appear to be developed in two ways, according to the size of the vessels. In the formation of large blood-vessels, masses of embryonic cells similar to those from which the heart and other structures of the embryo are developed, arrange themselves in the position, form, and thick-

ness of the developing vessel. Shortly afterwards the cells in the interior of a column of this kind seem to be developed into blood-corpuscles, while the external layer of cells is converted into the walls of the vessel.

In the development of capillaries another plan is pursued. This has been well illustrated by Kölliker, as observed in the tails of tadpoles. The first lateral vessels of the tail have the form of simple arches, passing between the main artery and vein, and are produced by the junction of prolongations, sent from both the artery and vein, with certain elongated or star-shaped cells, in the substance of the tail. When these arches are formed and are permeable to blood, new prolongations pass from them, join other radiated cells, and thus form secondary arches (fig. 363). In this manner, the capillary net-work extends in proportion as the tail increases in length and breadth, and it, at the same time, becomes more dense by the formation, according to the same plan, of fresh vessels within its meshes. The prolongations

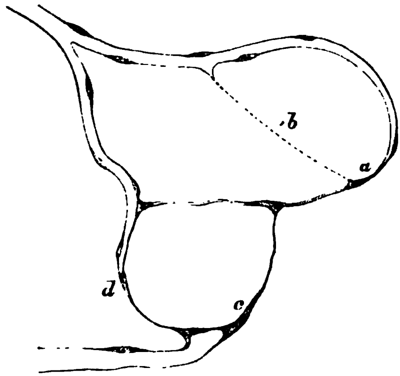
*Fig. 363.**



* Fig. 363. Capillary blood-vessels of the tail of a young larval frog. Magnified 350 times (Kölliker).—*a*, capillaries permeable to blood; *b*, fat-granules attached to the walls of the vessels, and concealing the nuclei; *c*, hollow prolongation of a capillary, ending in a point; *d*, a branching cell with nucleus and fat-granules; it communicates by three branches with prolongation of capillaries already formed; *e*, *e*, blood-corpuscles still containing granules of fat.

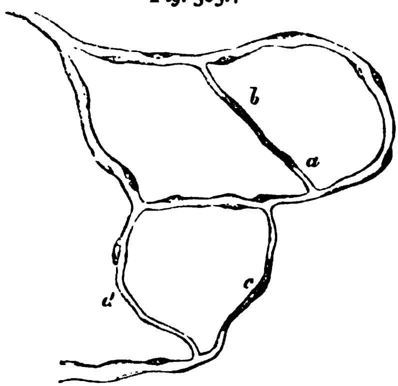
by which the vessels communicate with the star-shaped cells, consist at first of narrow-pointed projections from the side

Fig. 364.*



of the vessels, which gradually elongate until they come in

Fig. 365.†



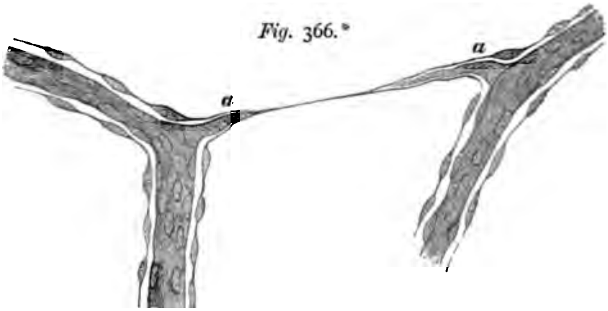
contact with the radiated processes of the cells. The thickness of such a prolongation often does not exceed that of a fibril

* Fig. 364. Development of capillaries in the regenerating tail of a tadpole. *a*, *b*, *c*, *d*, sprouts and cords of protoplasm (Arnold).

† Fig. 365. The same region after the lapse of 24 hours. The "sprouts and cords of protoplasm" have become channelled out into capillaries (Arnold).

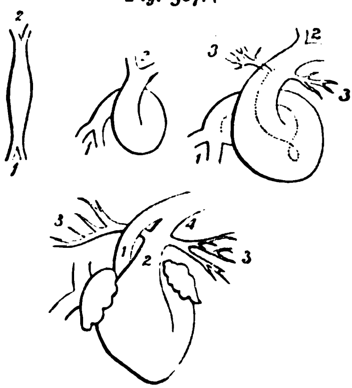
of fibrous tissue, and at first it is perfectly solid; but, by degrees, especially after its junction with a cell, or with another prolongation, or with a vessel already permeable to blood, it enlarges, and a cavity then forms in its interior (see figs. 364, 365, 366). This

Fig. 366.*



tissue is well calculated to illustrate the various steps in the development of blood-vessels from elongating and branching cells.

Fig. 367.†



Morphology. Heart.—When it first appears, the heart is approximately tubular in form. It receives at its two posterior angles the two omphalo-mesenteric veins, and gives off anteriorly the primitive aorta (fig. 367).

It soon, however, becomes curved somewhat in the shape of a horse-shoe, with the convexity towards the right, the venous end being at the same time drawn up towards the head, so that it finally lies behind

* Fig. 366. Capillaries from the vitreous humour of a fœtal calf. Two vessels are seen connected by a "cord" of protoplasm, and clothed with an adventitia, containing numerous nuclei. *a*, insertion of this "cord" into the primary wall of the vessels (Frey).

† Fig. 367. Fœtal heart in successive stages of development. 1, venous extremity; 2, arterial extremity; 3, 3, pulmonary branches; 4, ductus arteriosus (Dalton).

and somewhat to the right of the arterial. It also becomes partly divided by constrictions into three cavities.

Of these three cavities which are developed in all Vertebrata, that at the venous end is the simple auricle, that at the arterial end the bulbus arteriosus, and the middle one is the simple ventricle.

These three parts of the heart contract in succession. The auricle and the bulbus arteriosus at this period lie at the extremities of the horse-shoe. The bulging out of the middle portion inferiorly gives the first indication of the future form of the ventricle (fig. 368). The great curvature of the horse-shoe by

Fig. 368.*

the same means becomes much more developed than the smaller curvature between the auricle and bulbus; and the two extremities, the auricle and bulb, approach each other superiorly, so as to produce a greater resemblance to the later form of the heart, whilst the ventricle becomes more and more developed inferiorly. The heart of Fishes retains these three cavities, no further division by internal septa into right and left chambers taking place. In Amphibia, also, the heart throughout life consists of the three muscular divisions which are so early formed in the embryo; but the auricle is divided internally by a septum into a pulmonary and systemic auricle. In Reptiles, not merely the auricle is thus divided into two cavities, but a similar septum is more or less developed in the ventricle. In Birds and Mammals, both auricle and ventricle undergo complete division by septa; whilst in these animals as well as in reptiles, the bulbus aortæ is not permanent, but becomes lost in the ventricles. The septum dividing the ventricle com-

* Fig. 368. Heart of the chick at the 45th, 65th, and 85th hours of incubation. 1, the venous trunks; 2, the auricle; 3, the ventricle; 4, the bulbus arteriosus (Allen Thomson).

mences at the apex and extends upwards. The sub-division of the auricles is very early foreshadowed by the outgrowth of the two auricular appendages, which occurs before any septum is formed externally. The septum of the auricles is developed from a semilunar fold, which extends from above downwards. In man, the septum between the ventricles, according to Meckel, begins to be formed about the fourth week, and at the end of eight weeks is complete. The septum of the auricles, in man and all animals which possess it, remains imperfect throughout fœtal life. When the partition of the auricles is first commencing, the two venæ cavæ have different relations to the two cavities. The superior cava enters, as in the adult, into the right auricle; but the inferior cava is so placed that it appears to enter the left auricle, and the posterior part of the septum of the auricles is formed by the Eustachian valve, which extends from the point of entrance of the inferior cava. Subsequently, however, the septum, growing from the anterior wall close to the upper end of the ventricular septum, becomes directed more and more to the left of the vena cava inferior. During the entire period of fœtal life, there remains an opening in the septum, which the valve of the foramen ovale, developed in the third month, imperfectly closes.

The *bulbus arteriosus* which is originally a single tube, becomes gradually divided into two by the growth of an internal septum, which springs from the posterior wall, and extends forwards towards the front wall and downwards towards the ventricles. This partition takes a somewhat spiral direction, so that the two tubes (aorta and pulmonary artery) which result from its completion, do not run side by side, but are twisted round each other.

As the septum grows down towards the ventricles, it meets and coalesces with the upwardly growing ventricular septum, and thus from the right and left ventricles, which are now completely separate, arise respectively the pulmonary artery and aorta, which are also quite distinct. The auriculo-ventricular and semilunar valves are formed by the growth of folds of the endocardium.

At its first appearance the heart is placed just beneath the

head of the fœtus, and is very large relatively to the whole body: but with the growth of the neck it becomes further and further removed from the head, and lodged in the cavity of the thorax.

Up to a certain period the auricular is larger than the ventricular division of the heart; but this relation is gradually reversed as development proceeds. Moreover, all through fœtal life, the walls of the right ventricle are of very much the same thickness as those of the left, which may probably be explained by the fact that in the fœtus the right ventricle has to propel the blood from the pulmonary artery into the aorta, and thence into the placenta, while in the adult it only drives the blood through the lungs.

Arteries.—The primitive aorta arises from the bulbus arteriosus and divides into two branches which arch backwards, one on each side of the foregut and unite again behind it, and in front of the notochord into a single vessel.

This gives off the two omphalo-mesenteric arteries, which distribute branches all over the yolk-sac; this *area vasculosa* in the chick attaining a large development, and being limited all round by a vessel known as the sinus terminalis.

The blood is collected by the venous channels, and returned through the omphalo-mesenteric veins to the heart.

Behind this pair of primitive aortic arches, four more pairs make their appearance successively, so that there are five pairs in all, each one running along one of the visceral arches.

These five are never all to be seen at once in the embryo of higher animals, for the two anterior pairs gradually disappear, while the posterior ones are making their appearance, so that at length only three remain.

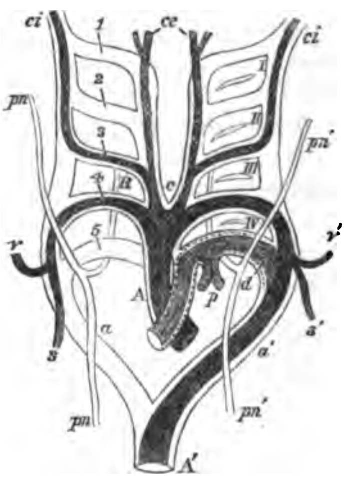
In Fishes, however, they all persist throughout life as the branchial arteries supplying the gills, while in Amphibia three pairs persist throughout life.

In Reptiles, Birds, and Mammals, further transformations occur.

In Reptiles the fourth pair remains throughout life as the permanent right and left aorta; in Birds the right one remains as the permanent aorta, curving over the right bronchus instead of the left as in Mammals.

In Mammals the left fourth aortic arch developes into the permanent aorta, the right one remaining as the subclavian artery of that side. Thus the subclavian artery on the right side corresponds to the aortic arch on the left, and this homology is further confirmed by the fact that the recurrent laryngeal nerve hooks under the subclavian on the right side, and the aortic arch on the left.

Fig. 369.*



The third aortic arch remains as the external carotid artery, while the fifth disappears on the right side, but on the left forms the pulmonary artery. The distal end of this arch originally opens into the descending aorta, and this communication (which is permanent throughout life in many reptiles on both sides of the body) remains throughout fœtal life under the name of *ductus arteriosus:* the branches of the pulmonary artery to the

* Fig. 369. Diagram of the aortic arches in a mammal, showing transformations which give rise to the permanent arterial vessels. *A*, primitive arterial stem or aortic bulb, now divided into *A*, the ascending part of the aortic arch, and *p*, the pulmonary; *a a'*, right and left aortic roots; *A'*, descending aorta; 1, 2, 3, 4, 5, the five primitive aortic or branchial arches; *I, II, III, IV*, the four branchial clefts which, for the sake of clearness, have been omitted on the right side. The permanent systemic vessels are deeply, the pulmonary arteries, lightly shaded; the parts of the primitive arches which are transitory are simply outlined; *c*, placed between the permanent common carotid arteries; *c e*, external carotid arteries; *c i*, internal carotid arteries; *s*, right subclavian, rising from the right aortic root beyond the fifth arch; *v*, right vertebral from the same, opposite the fourth arch; *v' s'*, left vertebral and subclavian arteries rising together from the left, or permanent aortic root, opposite the fourth arch; *p*, pulmonary arteries rising together from the left fifth arch; *d*, outer or back part of left fifth arch, forming ductus arteriosus; *p n*, *p n'*, right and left pneumogastric nerves, descending in front of aortic arches, with their recurrent branches represented diagrammatically as passing behind, to illustrate the relations of these nerves respectively to the right subclavian artery (4), and the arch of the orta and ductus arteriosus (*d*) (Allen Thomson, after Rathke).

right and left lung are very small, and most of the blood which is forced into the pulmonary artery passes through the wide ductus arteriosus into the descending aorta. All these points will become clear on reference to the accompanying diagram (fig. 369).

As the umbilical vesicle dwindles in size, the portion of the omphalo-mesenteric arteries outside the body gradually disappears, the part inside the body remaining as the mesenteric arteries (figs. 370, 371).

Fig. 370.*

Fig. 371.†

Meanwhile with the growth of the allantois two new arteries (umbilical) appear, and rapidly increase in size till they are the largest branches of the aorta: they are given off from the internal iliac arteries, and for a long time are considerably larger than the external iliacs which supply the comparatively small hind-limbs.

Veins.—The chief veins in the early embryo may be divided

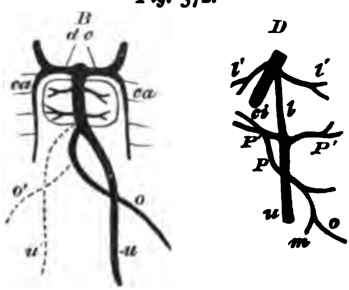
* Fig. 370. Diagram of young embryo and its vessels, showing course of circulation in the umbilical vesicle; and also that of the allantois (near the caudal extremity), which is just commencing (Dalton).

† Fig. 371. Diagram of embryo and its vessels at a later stage, showing the second circulation. The pharynx, œsophagus, and intestinal canal have become further developed, and the mesenteric arteries have enlarged, while the umbilical vesicle and its vascular branches are very much reduced in size. The large umbilical arteries are seen passing out in the placenta (Dalton).

into two groups, visceral and parietal: the former includes the omphalo-mesenteric and umbilical, the latter the jugular and cardinal veins. The former may be first considered.

The earliest veins to appear in the fœtus are the omphalo-mesenteric which return the blood from the yolk-sac to the developing auricle. As soon as the placenta with its umbilical veins is developed, these unite with the omphalo-mesenteric, and thus the blood which reaches the auricle comes partly from the yolk-sac and partly from the placenta. The right omphalo-mesenteric and the right umbilical vein soon disappear, and the united left omphalo-mesenteric and umbilical veins pass through the developing liver on their way to the auricle. Two sets of vessels make their appearance in connection with the liver (venæ hepaticæ advehentes, and revehentes), both opening into the united omphalo-mesenteric and umbilical veins, in such a way that a portion of the venous blood traversing the latter is diverted into the developing liver, and, having passed through its capillaries, returns to the umbilical vein through the venæ hepaticæ revehentes at a point nearer the heart (see fig. 372). The portion of vein between the afferent and efferent veins of the liver becomes the ductus venosus. The venæ hepaticæ advehentes become the right and left branches of the portal vein, the venæ hepaticæ revehentes become the hepatic veins, which open just at the junction of the ductus venosus with another large vein

Fig. 372.*



* Fig. 372. Diagrams illustrating the development of veins about the liver. *B*, *d c*, ducts of Cuvier, right and left; *c a*, right and left cardinal veins; *o*, left omphalo-mesenteric vein; *o'* right omphalo-mesenteric vein, almost shrivelled up; *u*, *u'*, umbilical veins, of which *u'*, the right one, has almost disappeared. Between the venæ cardinales is seen the outline of the rudimentary liver, with its venæ hepaticæ advehentes, and revehentes; *D*, ductus venosus; *l'*, hepatic veins; *c i*, vena cava inferior; *P*, portal vein; *P' P'*, venæ advehentes; *m*, mesenteric veins (Kölliker).

(vena cava inferior), which is now being developed. The mesenteric portion of the omphalo-mesenteric vein returning blood from the developing intestines remains as the mesenteric vein, which, by its union with the splenic vein, forms the portal.

Thus the fœtal liver is supplied with venous blood from two sources, through the umbilical and portal vein respectively. At birth the circulation through the umbilical vein of course completely ceases and the vessel begins at once to dwindle. so that now the only venous supply of the liver is through the portal vein. The earliest appearance of the *parietal* system of veins is the formation of two short transverse veins (ducts of Cuvier) opening into the auricle on either side, which result from the union of a jugular vein, collecting blood from the head and neck, and a cardinal vein which returns the blood from the Wolffian bodies, the vertebral column, and the parietes of the trunk. This arrangement persists throughout life in Fishes, but in Mammals the following tranformations occur.

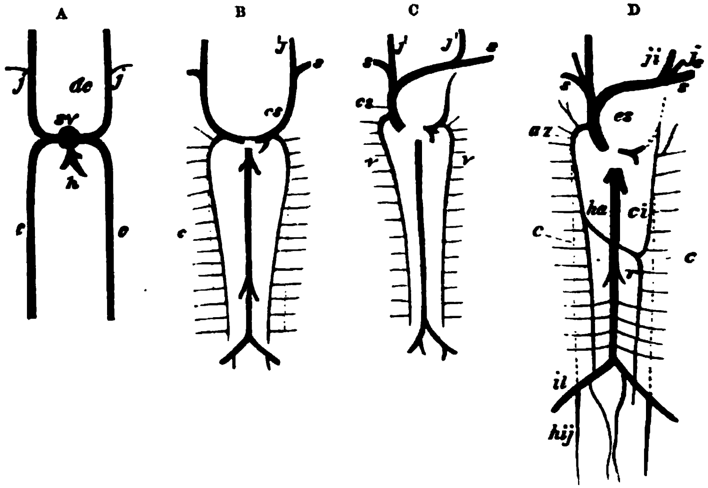
As the kidneys are developing a new vein appears (vena cava inferior), formed by the junction of their efferent veins. It receives branches from the legs (iliac) and increases rapidly in size as they grow: further up it receives the hepatic veins. The heart gradually descends into the thorax causing the ducts of Cuvier to become oblique instead of transverse. As the fore-limbs develop, the subclavian veins are formed.

A transverse communicating trunk now unites the two ducts of Cuvier, and gradually increases, while the left duct of Cuvier becomes almost entirely obliterated (all its blood passing by the communicating trunk to the right side) (fig. 373, C, D). The right duct of Cuvier remains as the right innominate vein, while the communicating branch forms the left innominate. The remnant of the left duct of Cuvier generally remains as a fibrous band, running obliquely down to the coronary vein, which is really the proximal part of the left duct of Cuvier. In front of the root of the left lung, another relic may be found in the form of the so-called vestigial fold of Marshall, which is a fold of pericardium running in the same direction.

In many of the lower mammals, such as the rat, the left ductus Cuvieri remains as a left superior cava.

Meanwhile, a transverse branch carries across most of the blood of the left cardinal vein into the right: and by this union the great azygos vein is formed.

Fig. 373.*



The upper portions of the left cardinal vein remain as the left superior intercostal and vena azygos minor (fig. 373, D).

Circulation of Blood in the Fœtus.

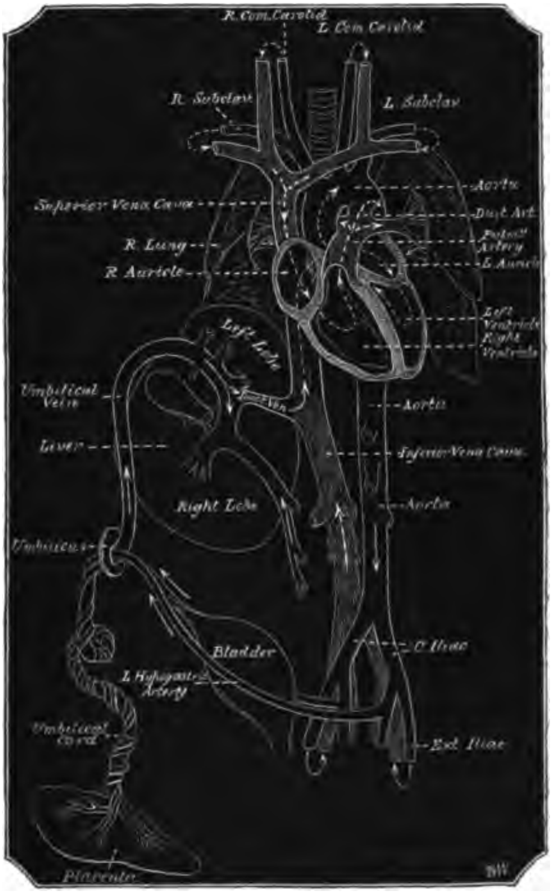
The circulation of blood in the fœtus differs considerably from that of the adult. It will be well, perhaps, to begin its description by tracing the course of the blood, which, after being carried out to the placenta by the two umbilical *arteries*, has returned, cleansed and replenished, to the fœtus by the umbilical vein.

It is at first conveyed to the under surface of the liver, and there the stream is divided,—a part of the blood passing straight

* Fig. 373. Diagrams illustrating the development of the great veins. *d c*, ducts of Cuvier; *j*, jugular veins; *h*, hepatic veins; *c*, cardinal veins; *s*, subclavian vein; *j i*, internal jugular vein; *j e*, external jugular vein; *a z*, azygos vein; *c i*, inferior vena cava; *r*, renal veins; *i l*, iliac veins; *h i j*, hypogastric veins (Gegenbaur).

on to the *inferior* vena cava, through a venous canal called the *ductus venosus*, while the remainder passes into the portal vein, and reaches the inferior vena cava only after circulating through

Fig. 374.*



the liver. Whether, however, by the direct route through the ductus venosus or by the roundabout way through the liver,—all

* Fig. 374. Diagram of the Fœtal Circulation.

the blood which is returned from the placenta by the umbilical vein reaches the inferior vena cava at last, and is carried by it to the right auricle of the heart, into which cavity is also pouring the blood that has circulated in the head and neck and arms, and has been brought to the auricle by the *superior* vena cava. It might be naturally expected that the two streams of blood would be mingled in the right auricle, but such is not the case, or only to a slight extent. The blood from the *superior* vena cava,—the less pure fluid of the two—passes almost exclusively into the *right* ventricle, through the auriculo-ventricular opening, just as it does in the adult; while the blood of the *inferior* vena cava is directed by a fold of the lining membrane of the heart, called the *Eustachian valve*, through the foramen ovale into the *left* auricle, whence it passes into the *left* ventricle, and out of this into the aorta, and thence to all the body. The blood of the *superior* vena cava, which, as before said, passes into the right ventricle, is sent out thence in small amount through the pulmonary artery to the lungs, and thence to the *left* auricle, as in the adult. The greater part, however, by far, does not go to the lungs, but instead, passes through a canal, the *ductus arteriosus*, leading from the pulmonary artery into the aorta just below the origin of the three great vessels which supply the upper parts of the body; and there meeting that part of the blood of the inferior vena cava which has not gone into these large vessels, it is distributed with it to the trunk and lower parts,—a portion passing out by way of the two umbilical *arteries* to the placenta. From the placenta it is returned by the umbilical *vein* to the under surface of the liver, from which the description started.

After birth the foramen ovale closes, and so do the ductus arteriosus and ductus venosus, as well as the umbilical vessels; so that the two streams of blood which arrive at the right auricle by the superior and inferior vena cava respectively, thenceforth mingle in this cavity of the heart, and passing into the right ventricle, go by way of the pulmonary artery to the lungs, and through these, after purification, to the left auricle and ventricle, to be distributed over the body. (See Chapter on Circulation.)

Development of the Nervous System.

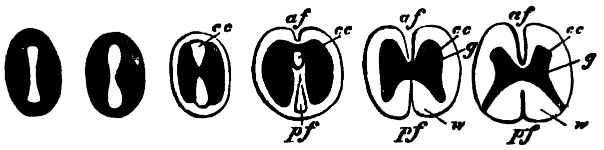
Nerves.—All the spinal nerves are derived from the mesoblast; also all the cranial nerves, except the optic and olfactory, which are outgrowths of the anterior cerebral vesicles. From the same middle layer of the embryo are also derived the ganglia connected with these nerves, and the whole sympathetic system of nerves and ganglia.

Spinal Cord.—Both the brain and spinal cord have a different origin from that of the nerves which arise from them. These nerve-centres are developed entirely from the epiblast (possibly, however, a portion of the spinal cord originates in the mesoblast), while the nerves, as we have seen, are formed from mesoblast. The spinal cord is developed out of the primitive medullary tube which results from the folding in of the dorsal laminæ (*m*, fig. 341).

Soon after it has closed in, this tube is found to be somewhat oval in section, with a central canal, which, in sections, presents the appearance of an elongated slit, slightly expanded at each end. The two opposite sides unite (fig. 375) in the centre of the slit, dividing it into an anterior portion (the permanent central canal of the cord) and a posterior, which makes its way to the free surface, and persists as the posterior fissure of the cord, lodging a very fine process of pia mater.

At this period the cord consists almost entirely of grey matter,

Fig. 375.*



but the white matter, which is derived probably from the surrounding mesoblast, becomes deposited around it on all sides, growing up especially on the anterior surface of the cord into

* Fig. 375. Diagram of development of spinal cord; *cc*, central canal; *af*, anterior fissure; *pf*, posterior fissure; *g*, grey matter; *w*, white matter. *For further explanation see text.*

the two anterior columns. These are separated by a fissure (anterior fissure of cord), which of course deepens as the columns bounding it become more prominent (fig. 375).

By the development of various commissures, the cord is completed.

When it first appears, the spinal cord occupies the whole length of the medullary canal, but as development proceeds, the spinal column grows more rapidly than the contained cord, so that the latter appears as if drawn up till, at birth, it is opposite the third lumbar vertebra, and in the adult opposite the first lumbar. In the same way the increasing obliquity of the spinal nerves in the neural canal, as we approach the lumbar region, and the "cauda equina" at the lower end of the cord, are accounted for.

Brain.—We have seen (p. 748) that the front portion of the medullary canal is almost from the first widened out and divided into three vesicles. From the anterior vesicle (thalamencephalon) the two primary optic vesicles are budded off laterally: their further history will be traced in the next section. Somewhat later, from the same vesicle the rudiments of the hemispheres appear in the form of two outgrowths at a higher level, which grow upwards and backwards. These form the *prosencephalon.*

In the walls of the posterior (third) cerebral vesicle, a thickening appears (rudimentary cerebellum) which becomes separated from the rest of the vesicle by a deep inflection.

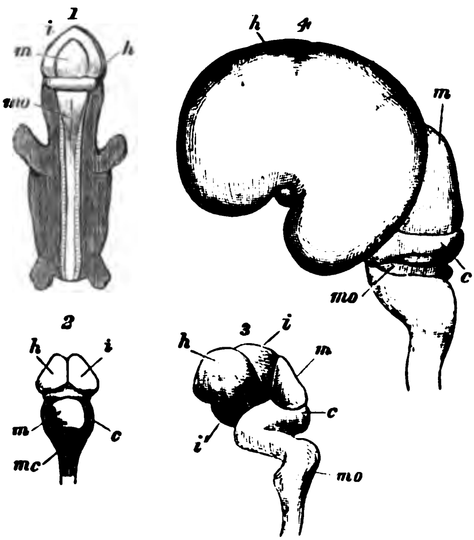
At this time there are two chief curvatures of the brain (fig. 376, 3). (1). A sharp bend of the whole cerebral mass downwards round the end of the notochord, by which the anterior vesicle, which was the highest of the three, is bent downwards, and the middle one comes to occupy the highest position. (2). A sharp bend, with the convexity forwards, which runs in from behind beneath the rudimentary cerebellum separating it from the medulla.

Thus, five fundamental parts of the fœtal brain may be distinguished, which, together with the parts developed from them may be presented in the following tabular view.

I. Anterior Primary Vesicle.	1. Prosencephalon.	Cerebral hemispheres, corpora striata, corpus callosum, fornix, lateral ventricles, olfactory bulb (Rhinencephalon).
	2. Thalamencephalon (Diencephalon).	Thalami optici, pineal gland, pituitary body, third ventricle, optic nerve (primarily).
II. Middle Primary Vesicle.	3. Mesencephalon.	Corpora quadrigemina, crura cerebri, aqueduct of Sylvius, optic nerve (secondarily).
III. Posterior Primary Vesicle.	4. Epencephalon.	Cerebellum, pons Varolii, anterior part of fourth ventricle.
	5. Metencephalon.	Medulla oblongata, fourth ventricle, auditory nerve.

(*Quain's Anatomy.*)

Fig. 376.*



* Fig. 376. Early stages in development of human brain (magnified). 1, 2, 3, are from an embryo about seven weeks old; 4, about three months' old. *m*, middle cerebral vesicle (mesencephalon); *c*, cerebellum; *m o*, medulla oblongata; *i*, thalamencephalon; *h*, hemispheres; *i'*, infundibulum; Fig. 3 shows the several curves which occur in the course of development; Fig. 4 is a lateral view, showing the great enlargement of the cerebral hemispheres which have covered in the thalami, leaving the optic lobes, *m*, uncovered (Kölliker).

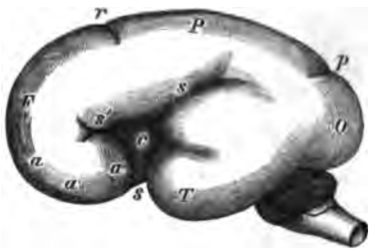
N.B. In Fig. 2 the line *i* terminates in the right hemisphere, it ought to be continued into the thalamencephalon.

The cerebral hemispheres grow rapidly upwards and backwards, while from their inferior surface the olfactory bulbs are budded off, and the thalamencephalon, from which they spring, remains to form the third ventricle and optic thalami. The middle cerebral vesicle (mesencephalon) for some time is the most prominent part of the fœtal brain, and in Fishes, Amphibia, and Reptiles, it remains uncovered through life as the optic lobes. But in Birds the growth of the cerebral hemispheres thrusts the optic lobes down laterally, and in Mammalia completely overlaps them.

In the lower Mammalia the backward growth of the hemispheres ceases as it were, but in the higher groups, such as the monkeys and man, they grow still further back, until they completely cover in the cerebellum, so that on looking down on the brain from above, the cerebellum is quite concealed from view. The surface of the hemispheres is at first quite smooth, but as early as the third month the great Sylvian fissure begins to be formed (fig. 376, 4).

The next to appear is the parieto-occipital or perpendicular fissure; these two great fissures, unlike the rest of the sulci, are formed by a curving round of the whole cerebral mass.

Fig. 377.*

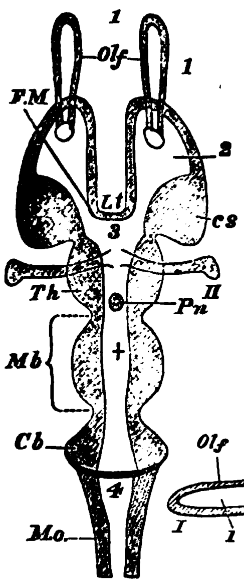


In the sixth month the fissure of Rolando appears: from this time till the end of fœtal life the brain grows rapidly in size, and the convolutions appear in quick succession; first the great primary ones are sketched out, then the secondary, and lastly the tertiary ones in the sides of the fissures. The commissures of the brain (anterior, middle, and

* Fig. 377. Side view of fœtal brain at six months, showing commencement of formation of the principal fissures and convolutions. *F*, frontal lobe; *P*, parietal; *O*, occipital; *T*, temporal; *a a a*, commencing frontal convolutions; *s*, Sylvian fissure; *s'*, its anterior division; *c*, within it the central lobe or island of Reil; *r*, fissure of Rolando; *p*, perpendicular fissure (R. Wagner).

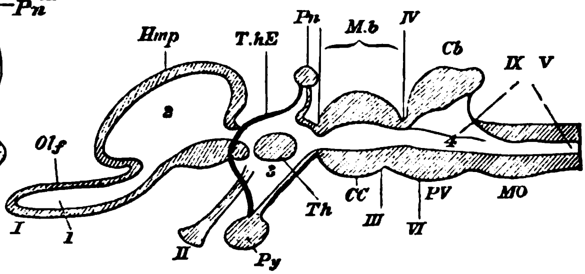
posterior), and the corpus callosum, are developed by the growth of fibres across the middle line.

Fig. 378.*



The Hippocampus major is formed by the folding in of the grey matter from the exterior into the lateral ventricles. The essential points in the structure and arrangement of the various parts of the brain, are diagrammatically shown in the two accompanying figures (figs. 378, 379).

Fig. 379.†



Development of the Organs of Sense.

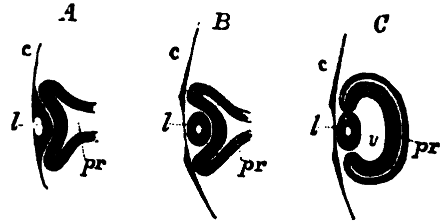
Eye.—Soon after the first three cerebral vesicles have become distinct from each other, the anterior one sends out a lateral vesicle from each side, (primary optic vesicle), which grows out

* Fig. 378. Diagrammatic horizontal section of a Vertebrate brain. The figures serve both for this and the next diagram. *Mb*, mid brain: what lies in front of this is the fore-, and what lies behind, the hind-brain; *Lt*, lamina terminalis; *Olf*, olfactory lobes; *Hmp*, hemispheres; *Th.E*, thalamencephalon; *Pn*, pineal gland; *Py*, pituitary body; *FM*, foramen of Munro; *cs*, corpus striatum; *Th*, optic thalamus; *CC*, crura cerebri: the mass lying above the canal represents the corpora quadrigemina; *Cb*, cerebellum; *I—IX.*, the nine pairs of cranial nerves; 1, olfactory ventricle; 2, lateral ventricle; 3, third ventricle; 4, fourth ventricle; +, iter a tertio ad quartum ventriculum (Huxley).

† Fig. 379. Longitudinal and vertical diagrammatic section of a *Vertebrate brain.* Letters as before. Lamina terminalis is represented by the strong black line joining *Pn* and *Py* (Huxley).

towards the free surface, its cavity of course communicating with that of the cerebral vesicle through the canal in its pedicle. It is soon met and invaginated by an in-growing process from

Fig. 380.*



the epiblast (fig. 380), very much as the growing tooth is met by the process of epithelium which produces the enamel organ. This process of the epiblast is at first a depression which ultimately becomes closed in at the edges so as to produce a hollow ball, which is thus completely severed from the epithelium with which it was originally continuous. From this hollow ball the crystalline lens is developed. By the ingrowth of the lens the anterior wall of the primary optic vesicle is forced back nearly into contact with the posterior, and thus the primary optic vesicle is almost obliterated. The cells in the anterior wall are much longer than those of the posterior wall; from the former the retina is developed, from the latter the choroid.

The cup-shaped hollow in which the lens is now lodged is termed the secondary optic vesicle : its walls grow up all round, leaving, however, a slit at the lower part.

Through this slit (fig. 382), often termed the *choroidal fissure*, a process of mesoblast containing numerous blood-vessels projects, and occupies the cavity of the secondary optic vesicle behind the lens, filling it with vitreous humour and furnishing the lens

* Fig. 380. Longitudinal section of the primary optic vesicle in the chick magnified (from Remak).—A, from an embryo of sixty-five hours; B, a few hours later; C, of the fourth day; *c*, the corneous layer or epidermis, presenting in A, the open depression for the lens, which is closed in B and C; *l*, the lens follicle and lens; *pr*, the primary optic vesicle; in A and B, the pedicle is shown; in C, the section being to the side of the pedicle, the latter is not shown; *v*, the secondary ocular vesicle and vitreous humour.

capsule and the capsulo-pupillary membrane. This process in Mammals projects, not only into the secondary optic vesicle, but also into the pedicle of the primary optic vesicle invaginating it

Fig. 381.*

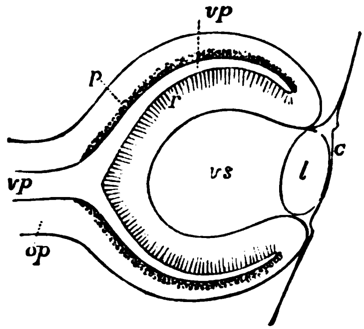
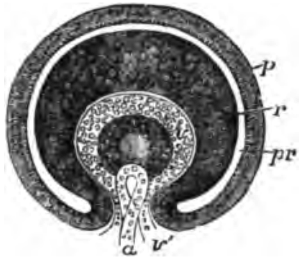


Fig. 382.†



for some distance from beneath, and thus carrying up the *arteria centralis retinæ* into its permanent position in the centre of the optic nerve.

This invagination of the optic nerve does not occur in *birds*, and consequently no arteria centralis retinæ exists in them. But they possess an important permanent relic of the original protrusion of the mesoblast through the choroidal fissure, forming the *pecten*, while a remnant of the same fissure sometimes occurs in man under the name coloboma iridis. The cavity of

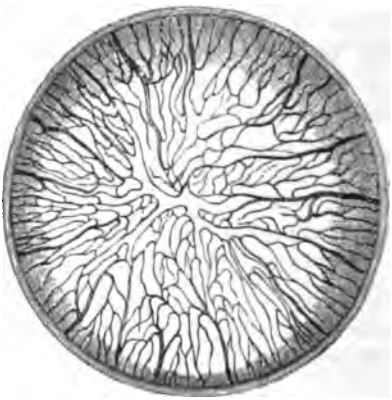
* Fig. 381. Diagrammatic sketch of a vertical longitudinal section through the eyeball of a human fœtus of four weeks (Kölliker) $\frac{100}{1}$.—The section is a little to the side, so as to avoid passing through the ocular cleft; *c*, the cuticle where it becomes later the cornea; *l*, the lens; *op*, optic nerve formed by the pedicle of the primary optic vesicle; *vp*, primary medullary cavity or optic vesicle; *p*, the pigment layer of the choroid coat of the outer wall; *r*, the inner wall forming the retina; *vs*, secondary optic vesicle containing the rudiment of the vitreous humour.

† Fig. 382. Transverse vertical section of the eyeball of a human embryo of four weeks (Kölliker) $\frac{100}{1}$.—The anterior half of the section is represented: *pr*, the remains of the cavity of the primary optic vesicle; *p*, the inner part of the outer layer forming the choroidal pigment; *r*, the thickened inner part giving rise to the columnar and other structures of the retina; *v*, the commencing vitreous humour within the secondary optic vesicle; *v'*, the ocular cleft through which the loop of the central blood-vessel, *a*, projects from below; *l*, the lens with a central cavity.

the primary optic vesicle becomes completely obliterated, and the retinal rods and cones come into apposition with the pigment of the choroid. The cavity of its pedicle disappears and the solid optic nerve is formed. Meanwhile the cavity which existed in the centre of the primitive lens becomes filled up by the growth of fibres from its posterior wall. The epithelium of the cornea is developed from the epiblast, while the corneal tissue proper is derived from the mesoblast which intervenes between the epiblast and the primitive lens which was originally continuous with it. The sclerotic coat is developed round the eye-ball from the general mesoblast in which it is embedded.

The iris is formed rather late, as a circular septum projecting inwards, from the fore part of the choroid, between the lens and the cornea. In the eye of the fœtus of Mammalia, the pupil is closed by a delicate membrane, the *membrana pupillaris*, which forms the front portion of a highly vascular membrane that, in the fœtus, surrounds the lens, and is named the *membrana*

Fig. 383.*



capsulo-pupillaris (fig. 383). It is supplied with blood by a branch of the *arteria centralis retinæ*, which, passing forwards

* Fig. 383. Blood-vessels, of the capsulo-pupillary membrane of a new-born kitten, magnified (Kölliker). The drawing is taken from a preparation injected by Tiersch, and shows in the central part the convergence of the net-work of vessels in the pupillary membrane.

to the back of the lens, there subdivides. The membrana capsulo-pupillaris withers and disappears in the human subject a short time before birth.

The eyelids of the human subject and mammiferous animals like those of birds, are first developed in the form of a ring. They then extend over the globe of the eye until they meet and become firmly agglutinated to each other. But before birth, or in the Carnivora after birth, they again separate.

Ear.—Very early in the development of the embryo a depression of the surface occurs on each side of the head which deepens and soon becomes a closed follicle. This *primary otic vesicle* which closely corresponds in its formation to the lens follicle in the eye, sinks down to some distance from the free surface; from it are developed the *membranous* labyrinth of the internal ear, consisting of the vestibule and its semicircular canals and the scala media of the cochlea. The surrounding mesoblast gives rise to the various bony and cartilaginous parts enclosing this membranous labyrinth, the bony semicircular canals, the walls of the cochlea with its scala vestibuli and scala tympani. In the mesoblast, between the primary otic vesicle and the brain, the auditory nerve is gradually differentiated and forms its central and peripheral attachments to the brain and internal ear respectively.

The Eustachian tube, the cavity of the tympanum, and the external auditory passage, are remains of the first branchial cleft. The membrana tympani divides the cavity of this cleft into an internal space, the tympanum, and the external meatus. The mucous membrane of the mouth, which is prolonged in the form of a diverticulum through the Eustachian tube into the tympanum, and the external cutaneous system, come into relation with each other at this point; the two membranes being separated only by the proper membrane of the tympanum.

The pinna or external ear is developed from a process of integument in the neighbourhood of the first and second visceral arches, and probably corresponds to the gill-cover (operculum) in fishes.

Nose.—The nose originates like the eye and ear in a depression of the superficial epiblast at each side of the fronto-nasal process (primary olfactory groove), which is at first completely separated from the cavity of the mouth, and gradually extends backwards and downwards till it opens into the mouth.

The outer angles of the fronto-nasal process, uniting with the maxillary process on each side, convert what was at first a groove into a closed canal.

Development of the Alimentary Canal.

The alimentary canal in the earliest stages of its development consists of three distinct parts—the fore and hind gut ending blindly at each end of the body, and a middle segment which communicates freely on its ventral surface with the cavity of the yelk-sac through the vitelline or omphalo-mesenteric duct (p. 753).

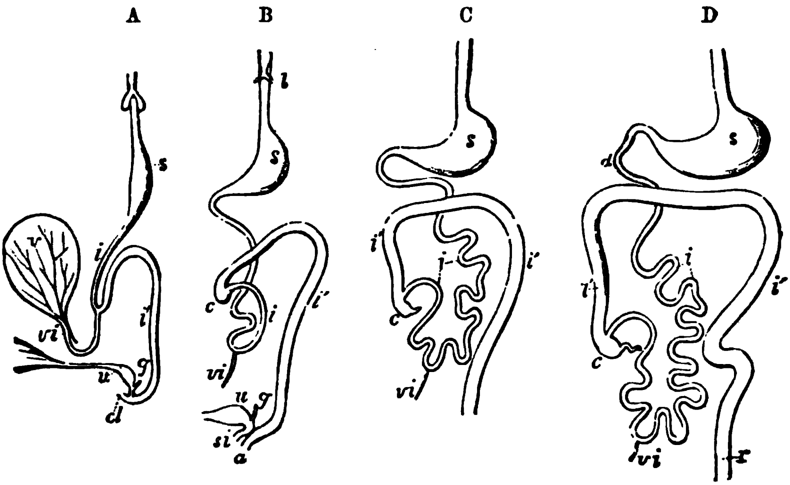
From the fore-gut are formed the pharynx, œsophagus, and stomach; from the hind-gut, the lower end of the colon and the rectum. The mouth is developed by an involution of the epiblast between the maxillary and mandibular processes, which becomes deeper and deeper till it reaches the blind end of the fore-gut, and at length communicates freely with the pharynx by the absorption of the partition between the two.

At the other end of the alimentary canal the anus is formed in a precisely similar way by an involution from the free surface, which at length opens into the hind-gut. When the depression from the free surface does not reach the intestine, the condition known as imperforate anus results. A similar condition may exist at the other end of the alimentary canal from the failure of the involution which forms the mouth, to meet the fore-gut. The middle portion of the digestive canal becomes more and more closed in till its originally wide communication with the yelk-sac becomes narrowed down to a small duct (vitelline). This duct usually completely disappears in the adult, but occasionally the proximal portion remains as a diverticulum from the intestine. Sometimes a fibrous cord attaching some part of the intestine to the umbilicus, remains to represent the vitelline duct.

Such a cord has been known to cause strangulation of the bowel and death.

The alimentary canal lies in the form of a straight tube close beneath the vertebral column, but it gradually becomes divided into its special parts, stomach, small intestine, and large intestine (fig. 384), and at the same time comes to be suspended in the abdominal cavity by means of a lengthening mesentery formed from the splanchnopleure which attaches it to the vertebral column. The stomach originally has the same direction as the rest of the canal; its cardiac extremity being superior, its pylorus inferior. The changes of position which the alimentary canal undergoes may be readily gathered from the accompanying figures.

Fig. 384.*



* Fig. 384. Outlines of the form and position of the alimentary canal in successive stages of its development. A, alimentary canal, &c., in an embryo of four weeks; B, at six weeks; C, at eight weeks; D, at ten weeks, ; *l*, the primitive lungs connected with the pharynx; *s*, the stomach; *d*, the duodenum; *i*, the small intestine; *i'*, the large; *c*, the cæcum and vermiform appendage; *r*, the rectum; *cl*, in A, the cloaca; *a*, in B, the anus distinct from *s i*, the sinus uro-genitalis; *v*, the yelk-sac; *v i*, the vitello-intestinal duct; *u*, the urinary bladder and urachus leading to the allantois; *g*, genital ducts (Allen Thomson).

The principal glands in connection with the intestinal canal are the salivary, pancreas, and the liver. In Mammalia, each salivary gland first appears as a simple canal with bud-like processes (fig. 385), lying in a gelatinous nidus or blastema, and communicating with the cavity of the mouth. As the development of the gland advances, the canal becomes more and more ramified, increasing at the expense of the blastema in which it is still enclosed. The branches or salivary ducts constitute an independent system of closed tubes (fig. 386). The pancreas is developed exactly as the salivary glands, but is developed from the hypoblast lining the intestine, while the salivary glands are formed from the epiblast lining the mouth.

Fig. 385.*

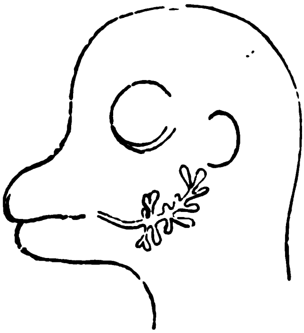


Fig. 386.†

The liver is developed by the protrusion, as it were, of a part of the walls of the intestinal canal, in the form of two conical hollow branches which embrace the common venous stem (figs. 387, 388). The outer part of these cones involves the omphalo-mesenteric

* Fig. 385. First appearance of the parotid gland in the embryo of a sheep.

† Fig. 386. Lobules of the parotid, with the salivary ducts, in the embryo of the sheep, at a more advanced stage.

Development of the Respiratory Apparatus.

The lungs, at their first development, appear as small tubercles, or diverticula from the abdominal surface of the œsophagus.

The two diverticula at first open directly into the œsophagus, but as they grow, a separate tube (the future trachea) is formed at their point of fusion, opening into the œsophagus on its anterior surface. These primary diverticula of the hypoblast of the alimentary canal send off secondary branches into the surrounding mesoblast, and these again give off tertiary branches, forming the air-cells. Thus we have the lungs formed: the epithelium lining their air-cells, bronchi, and trachea being derived from the hypoblast, and all the rest of the lung-tissue, nerves, lymphatics, and blood-vessels, cartilaginous rings and muscular fibres of the bronchi from the mesoblast. The diaphragm is early developed.

Fig. 389.*

A B C

The Wolffian Bodies, Urinary Apparatus, and Sexual Organs.

The Wolffian bodies are organs peculiar to the embryonic state, and may be regarded as *temporary*, rather than *rudimental*, kidneys; for although they seem to discharge the functions of these latter organs, they are not developed into them.

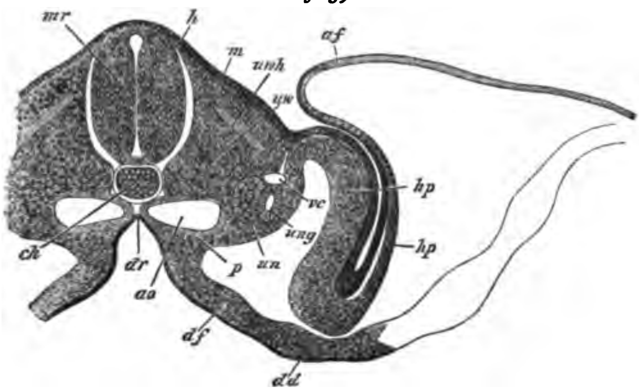
Appearance of first rudiments.

The Wolffian duct makes its appearance at an early stage in the history of the embryo, as a cord running longitudinally on

* Fig. 389, illustrates the development of the respiratory organs. A, is the œsophagus of a chick on the fourth day of incubation, with the rudiments of the trachea on the lung of the left side, viewed laterally: 1, the inferior wall of the œsophagus; 2, the upper wall of the same tube; 3, the rudimentary lung; 4, the stomach. B, is the same object seen from below, so that both lungs are visible. C, shows the tongue and respiratory organs of the embryo of a horse: 1, the tongue; 2, the larynx; 3, the trachea; 4, the lungs viewed from the upper side (after Rathke).

each side in the mass of mesoblast, which lies just external to the protovertebræ (*ung*, fig. 390). This cord, at first solid, be-

Fig. 390.*



comes gradually hollowed out to form a tube (Wolffian duct) which sinks down till it projects beneath the lining membrane into the pleuro-peritoneal cavity.

The primitive tube thus formed sends off secondary diverticula at frequent intervals, which grow into the surrounding mesoblast: tufts of vessels grow into the blind ends of these tubes, invaginating them and producing "Malpighian bodies" very similar in appearance to those of the permanent kidney, which constitute the substance of the Wolffian body. Meanwhile another portion of mesoblast between the Wolffian body and the mesentery projects in the form of a ridge, covered on its free surface with epithelium termed "germ epithelium." From this projection is developed the reproductive gland (ovary or testis as the case may be).

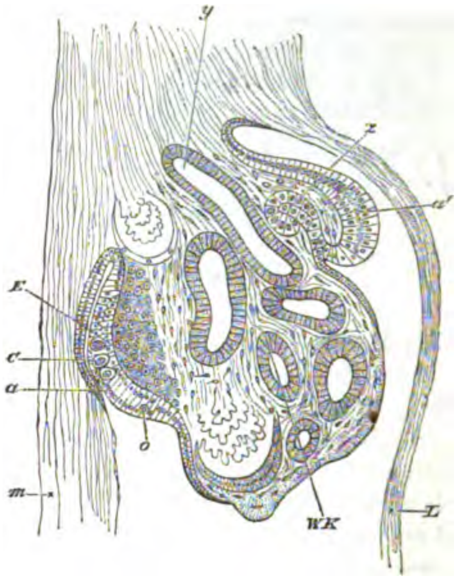
Simultaneously, on the outer side of the Wolffian body, between

* Fig. 390. Transverse of embryo chick (third day). *m r*, rudimentary spinal cord; the primitive central canal has become constricted in the middle; *c h*, notochord; *u w h*, primordial vertebral mass; *m*, muscle-plate; *dr*, *df*, hypoblast and visceral layer of mesoblast lining groove, which is not yet closed in to form the intestines; *a o*, one of primitive aortæ; *u n*, Wolffian body; *u n g*, Wolffian duct; *v c*, vena cardinalis; *h*, epiblast; *h p*, somatopleure and its reflection to form *a f*, amniotic fold; *p*, pleuroperitoneal cavity (Kölliker).

it and the body-wall on each side, an involution is formed from the pleuro-peritoneal cavity in the form of a longitudinal furrow, whose edges soon close over to form a duct (Müller's duct).

All the above points are shown in the accompanying figures, 391, 392, 394.

Fig. 391.*

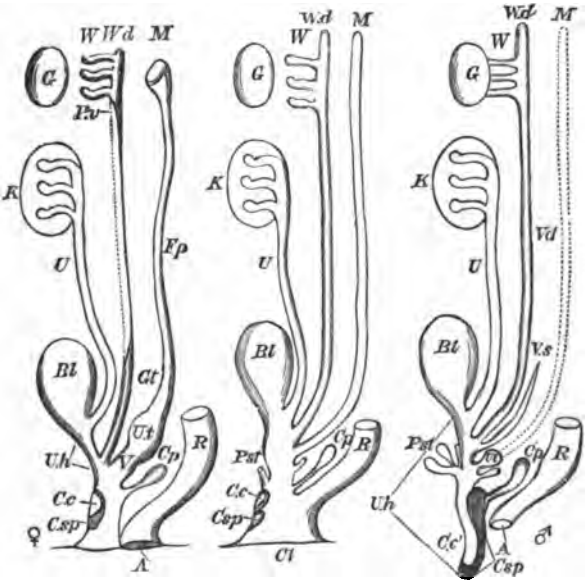


The Wolffian bodies, or *temporary* kidneys, as they may be termed, give place at an early period in the human fœtus to their successors, the *permanent* kidneys, which are developed behind them. They diminish rapidly in size, and by the end of the third month have almost entirely disappeared. In connection however, with their upper part, in the male, there are developed, from a new mass of blastema, the *vasa efferentia, coni vasculosi,*

* Fig. 391. Section of intermediate cell-mass on the fourth day. *m*, mesentery; *L*, somatopleure; *a'*, germinal epithelium, from which *z*, the duct of Müller, becomes involuted; *a*, thickened part of germinal epithelium, in which the primitive ova *C* and *o*, are lying; *E*, modified mesoblast, which will form the stroma of the ovary; *WK*, Wolffian body; *y*, Wolffian duct; × 160 (Waldeyer).

and *globus major* of the epididymis; and thus is brought about a direct connection between the secreting part of the testicle and its duct (Cleland, Banks). The Wolffian *ducts* persist in the male, and are developed to form the body and globus minor of the epididymis, the vas deferens, and ejaculatory duct on each side, the vesiculæ seminales forming diverticula from their lower part. In the female a small relic of the Wolffian body persists as the "parovarium," in the male a similar relic is termed the "organ of Giraldès." The lower end of the Wolffian duct remains in

Fig. 392.*



* Fig. 392. Diagram showing the relations of the female (the left-hand figure ♀) and of the male (the right hand figure ♂) reproductive organs to the general plan (the middle figure) of these organs in the higher vertebrata (including man). *Cl*, cloaca; *R*, rectum; *Bl*, urinary bladder; *U*, ureter; *K*, kidney; *Uh*, urethra; *G*, genital gland, ovary or testis; *W*, Wolffian body; *Wd*, Wolffian duct; *M*, Müllerian duct; *Pst*, prostate gland; *Cp*, Cowper's gland; *Csp*, corpus spongiosum; *Cc*, corpus cavernosum.

In the female.—*V*, vagina; *Ut*, uterus; *Fp*, Fallopian tube; *Gt*, Gaertner's duct; *Pv*, parovarium; *A*, anus; *Cc*, *Csp*, clitoris.

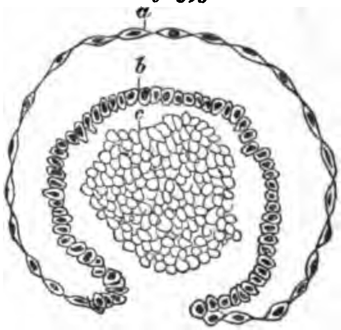
In the male.—*Csp*, *Cc*, penis; *Ut*, uterus masculinus; *Vs*, vesicula seminalis; *Vd*, vas deferens (Huxley).

the female as the "duct of Gaertner" which descends towards, and is lost upon, the anterior wall of the vagina.

From the lower end of the Wolffian duct a diverticulum grows back along the body of the embryo towards its anterior extremity, and ultimately forms the ureter. Secondary diverticula are given off from it and grow into the surrounding blastema of blood-vessels and cells.

Malpighian bodies are formed just as in the Wolffian body, by the invagination of the blind knobbed end of these diverticula by a tuft of vessels (fig. 393). This process is precisely similar to the invagination of the primary optic vesicle by the rudimentary lens. Thus the kidney is developed, consisting at first of a number of separate *lobules;* this condition remaining throughout life in many of the lower animals, *e.g.*, seals and whales, and traces of this lobulation being visible in the human fœtus at birth. In the adult all the lobules are fused into a compact solid organ.

Fig. 393.*



The supra-renal capsules originate in a mass of mesoblast just above the kidneys; soon after their first appearance they are very much larger than the kidneys (see fig. 394), but by the more rapid growth of the latter this relation is soon reversed.

Later Development.

The first appearance of the generative gland has been already described: for some time it is impossible to determine whether an ovary or testis will be developed from it; gradually however the special characters belonging to one of them appear, and in

* Fig. 393. Transverse section of a developing Malpighian capsule and tuft (human) × 300. From a fœtus at about the fourth month; *a*, flattened cells growing to form the capsule; *b*, more rounded cells, continuous with the above, reflected round *c*, and finally enveloping it; *c*, mass of embryonic cells which will later become developed into blood-vessels (W. Pye)

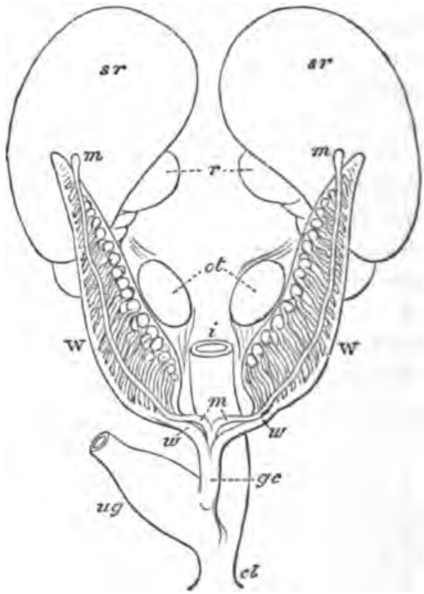
either case the organ soon begins to assume a relatively lower position in the body; the ovaries being ultimately placed in the pelvis; while towards the end of fœtal existence the testicles descend into the scrotum, the testicle entering the internal inguinal ring in the seventh month of fœtal life, and completing its descent through the inguinal canal and external ring into the scrotum by the end of the eighth month. A pouch of peritoneum, the *processus vaginalis*, precedes it in its descent, and ultimately forms the tunica vaginalis or serous covering of the organ; the communication between the tunica vaginalis and the cavity of the peritoneum being closed only a short time before birth. In its descent, the testicle or ovary of course retains the blood-vessels, nerves, and lymphatics, which were supplied to it while in the lumbar region, and which are compelled to follow it, so to speak, as it assumes a lower position in the body. Hence the explanation of the otherwise strange fact of the origin of these parts at so considerable a distance from the organ to which they are distributed.

The means by which the descent of the testicles into the scrotum is effected are not fully and exactly known. It was formerly believed that a membranous and partly muscular cord, called the *gubernaculum testis*, which extends while the testicle is yet high in the abdomen, from its lower part, through the abdominal wall (in the situation of the inguinal canal) to the front of the pubes and lower part of the scrotum, was the agent by the contraction of which the descent was effected. It is now generally believed, however, that such is not the case; and that the descent of the testicle and ovary is rather the result of a general process of development in these and neighbouring parts, the tendency of which is to produce this change in the relative position of these organs. In other words, the descent is not the result of a mere mechanical action, by which the organ is dragged down to a lower position, but rather one change out of many which attend the gradual development and re-arrangement of these organs. It may be repeated, however, that the details of the process by which the descent of the testicle into the scrotum is effected are not accurately known.

The homologue, in the female, of the gubernaculum testis, is a structure called the *round ligament of the uterus*, which extends through the inguinal canal, from the outer and upper part of the uterus to the subcutaneous tissue in front of the symphysis pubis.

At a very early stage of fœtal life, the Wolffian ducts, ureters, and Müllerian ducts, open into a receptacle formed by the lower end of the allantois, or rudimentary bladder; and as this communicates with the lower extremity of the intestine, there is for the time, a common receptacle or *cloaca* for all these parts, which opens to the exterior of the body through a part corresponding with the future anus, an arrangement which is perma-

Fig. 394.*



* Fig. 394. Diagram of the Wolffian bodies, Müllerian ducts and adjacent parts previous to sexual distinction, as seen from before. *sr*, the supra-renal bodies; *r*, the kidneys; *ot*, common blastema of ovaries or testicles; W, Wolffian bodies; *w*, Wolffian ducts; *m*, *m*, Müllerian ducts; *gc*, genital cord *ug*, sinus urogenitalis; *i*, intestine; *cl*, cloaca (Allen Thomson).

nent in Reptiles, Birds, and some of the lower Mammalia. In the human fœtus, however, the intestinal portion of the cloaca is cut off from that which belongs to the urinary and generative organs; a separate passage or canal to the exterior of the body, belonging to these parts, being called the *sinus urogenitalis*. Subsequently, this canal is divided, by a process of division extending from before backwards or from above downwards, into a 'pars urinaria' and a 'pars genitalis.' The former, continuous with the *urachus* (p. 757), is converted into the urinary bladder.

The Fallopian tubes, the uterus, and the vagina are developed from the Müllerian ducts (fig. 394, *m* and fig. 392) whose first appearance has been already described. The two Müllerian ducts are united below into a single cord, called the *genital cord*, and, from this are developed the vagina, as well as the cervix and the lower portion of the body of the uterus; while the ununited portion of the duct on each side forms the upper part of the uterus, and the Fallopian tube. In certain cases of arrested or abnormal development, these portions of the Müllerian ducts may not become fused together at their lower extremities, and there is left a cleft or horned condition of the upper part of the uterus resembling a condition which is permanent in certain of the lower animals.

In the male, the Müllerian ducts have no special function, and are but slightly developed. The hydatid of Morgagni is the remnant of the upper part of the Müllerian duct. The small prostatic pouch, *uterus masculinus*, or *sinus pocularis*, forms the atrophied remnant of the distal end of the genital cord, and is, of course, therefore, the homologue, in the male, of the vagina and uterus in the female.

The external parts of generation are at first the same in both sexes. The opening of the genito-urinary apparatus is, in both sexes, bounded by two folds of skin, whilst in front of it there is formed a penis-like body surmounted by a glans, and cleft or furrowed along its under surface. The borders of the furrow diverge posteriorly, running at the sides of the genito-urinary orifice internally to the cutaneous folds just mentioned

(see figs. 396, 398). In the female, this body becoming retracted, forms the clitoris, and the margins of the furrow on its under surface are converted into the nymphæ, or labia minora, the

Fig. 395 *

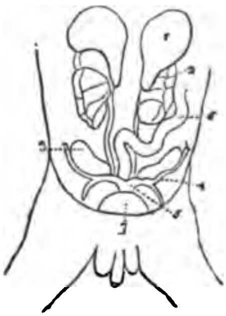


Fig. 396.

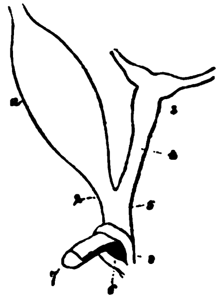


Fig. 397.

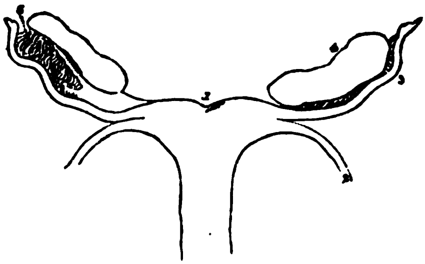
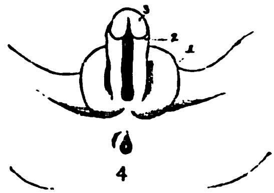


Fig. 398.



labia majora pudendæ being constituted by the great cutaneous folds. In the male fœtus, the margins of the furrow at the

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* Figs. 395, 396, 397, and 398. Urinary and generative organs of a human female embryo, measuring 3½ inches in length.

Fig. 395. General view of these parts; 1, supra-renal capsules; 2, kidneys; 3, ovary; 4, Fallopian tube; 5, uterus; 6, intestine; 7, the bladder.

Fig. 396. Bladder and Generative organs of the same embryo viewed from the side; *a*, the urinary bladder (at the upper part is a portion of the urachus); 2, urethra; 3, uterus (with two cornua); 4, vagina; 5, part as yet common to the vagina and urethra; 6, common orifice of the urinary and generative organs; 7, the clitoris.

Fig. 397. Internal generative organs of the same embryo; 1, the uterus; 2, the round ligaments; 3, the Fallopian tubes (formed by the Müllerian ducts); 4, the ovaries; 5, the remains of the Wolffian bodies.

Fig. 398. External generative organs of the same embryo; 1, the labia majora; 2, the nymphæ; 3, the clitoris; 4, anus (Müller).

under surface of the penis unite at about the fourteenth week, and form that part of the urethra which is included in the penis. The large cutaneous folds form the scrotum, and later (in the eighth month of development), receive the testicles, which descend into them from the abdominal cavity. Sometimes the urethra is not closed, and the deformity called hypospadias then results. The appearance of hermaphroditism may, in these cases, be increased by the retention of the testes within the abdomen.

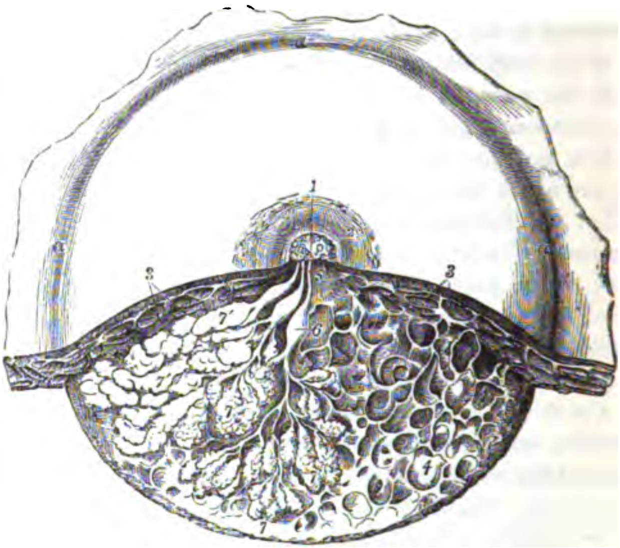
The Mammary Glands.

The mammary glands, which may be considered as organs superadded to the reproductive system in man and other members of the class (Mammalia) which derives its name from them, are, in the essential details of their structure, very similar to other compound glands, as the pancreas and salivary glands; that is to say, they are composed of larger divisions or lobes, and these are again divisible into lobules,—the lobules being composed of the follicular extremities of ducts, lined by glandular epithelium. The lobes and lobules are bound together by areolar tissue; while, penetrating between the lobes, and covering the general surface of the gland, with the exception of the nipple, is a considerable quantity of yellow fat, itself lobulated by sheaths and processes of tough areolar tissue (fig. 399) connected both with the skin in front and the gland behind; the same bond of connection extending also from the under surface of the gland to the sheathing connective tissue of the great pectoral muscle on which it lies. The main ducts of the gland, fifteen to twenty in number, called the *lactiferous* or *galactophorous* ducts, are formed by the union of the smaller ducts, and open by small separate orifices through the nipple. Just before they enter the base of the nipple, these ducts are dilated (6, fig. 399); and, during lactation, the period of active secretion by the gland, they form reservoirs for the milk, which collects in them and distends them. The walls of the gland-ducts are formed of areolar and elastic tissue, and are lined internally by a fine mucous membrane, the surface of which is covered by squamous or spheroidal epithelium.

The nipple, which contains the terminations of the lactiferous ducts, is composed also of areolar tissue, and contains unstriped muscular fibres. Blood-vessels are also freely supplied to it, so as to give it a species of erectile structure. On its surface are very sensitive papillæ; and around it is a small area or *areola* of pink or dark-tinted skin, on which are to be seen small projections formed by minute secreting glands.

Blood-vessels, nerves, and lymphatics are plentifully supplied to the mammary glands; the calibre of the blood-vessels, as well

Fig. 399.*



* Fig. 399. Dissection of the lower half of the female mamma during the period of lactation (from Luschka). ⅔.—In the left-hand side of the dissected part the glandular lobes are exposed and partially unravelled; and on the right-hand side, the glandular substance has been removed to show the reticular loculi of the connective tissue in which the glandular lobules are placed: 1, upper part of the mamilla or nipple; 2, areola; 3, subcutaneous masses of fat; 4, reticular loculi of the connective tissue which support the glandular substance and contain the fatty masses; 5, one of three lactiferous ducts shown passing towards the mamilla where they open; 6, one of the sinus lactei or reservoirs; 7, some of the glandular lobules which have been unravelled; 7', others massed together.

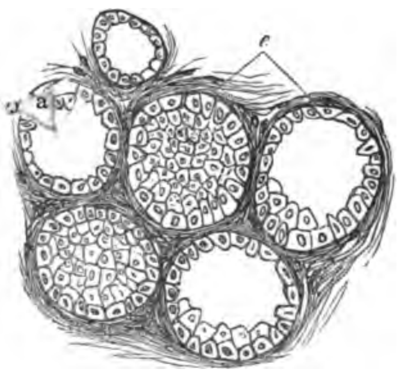
as the size of the glands, varying very greatly under certain conditions, especially those of pregnancy and lactation.

During pregnancy the mammary glands undergo changes which are readily observable. They enlarge, become harder and more distinctly lobulated: the veins on the surface become more prominent. The areola becomes enlarged and dusky, with projecting papillæ; the nipple too becomes more prominent, and milk can be squeezed from the orifices of the ducts.

The minute changes in the mammary gland during its periods of evolution (pregnancy), and involution (when lactation has ceased), have recently been investigated by Dr. Creighton. The following are the main points which have been ascertained by him and other observers:—

The most favourable period for observing the epithelium of the mammary gland fully developed, is shortly before the end of pregnancy. At this period the acini which form the lobules of the gland, are found to be lined with a mosaic of polyhedral epithelial cells (fig. 400), and supported by a connective tissue stroma.

*Fig. 400.**



Lactation.—The rapid formation of milk during this period results from a fatty metamorphosis of the epithelial cells:

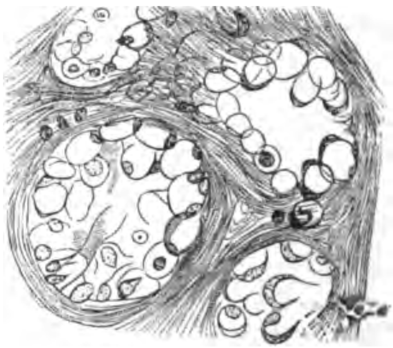
* Fig. 400. Section of mammary gland of rabbit near the end of pregnancy, showing six acini. *e*, epithelial cells of a polyhedral or short columnar form, with which the acini are packed; × 200 (Schofield).

"The secretion may be said to be produced by a transformation of the substance of successive generations of epithelial cells, and in the state of full activity this transformation is so complete that it may be called a deliquescence" (Creighton).

In the earlier days of lactation, epithelial cells partially transformed are discharged in the secretion: these are termed "colostrum corpuscles," but later on the cells are completely transformed before the secretion is discharged.

Involution.—After the end of lactation, the mamma gradually returns to its original size. The acini in the early stages of involution, are lined with cells in all degrees of vacuolation (fig. 401). As involution proceeds the acini diminish consider-

Fig. 401.*



ably in size, and at length, instead of a mosaic of lining epithelial cells (twenty to thirty in each acinus), we have five or six nuclei (some with no surrounding protoplasm) lying in an irregular heap within the acinus. During the later stages of involution, large yellow granular cells are to be seen. As the acini diminish in size, the connective tissue and fatty matter between them increase, and in some animals, when the gland is completely inactive, it is found to consist of a thin film of

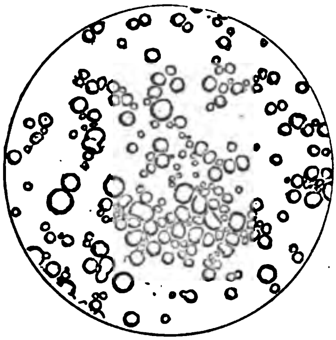
* Fig. 401. Section of mammary gland of ewe shortly after the end of lactation, showing parts of four acini, which contain numerous epithelial cells undergoing vacuolation *in situ*; they very closely resemble young fat-cells, and are in fact just like "colostrum corpuscles." × 300 (Creighton).

glandular tissue overlying a thick cushion of fat. Many of the products of waste are carried off by the lymphatics.

Evolution (Pregnancy).—This is a very gradual process, which commences about the time of conception, and progresses steadily during the whole period of gestation. The acini enlarge, and a series of changes occur, exactly the reverse of those just described under the head of Involution.

Under the microscope, milk is found to contain a number of globules of various size (fig. 402), the majority about $\frac{1}{10000}$ of

Fig. 402.*



an inch in diameter. They are composed of oily matter, probably coated by a fine layer of albuminous material, and are called *milk-globules*; while, accompanying these, are numerous minute particles, both oily and albuminous, which exhibit ordinary molecular movements. The milk, which is secreted in the first few days after parturition, and which is called the *colostrum*, differs from ordinary milk in containing a larger quantity of solid matter; and under the microscope are to be seen certain granular masses called *colostrum-corpuscles*. These, which appear to be small masses of albuminous and oily matter, are probably secreting cells of the gland, either in a state of fatty degeneration, or, as Dr. Gedge remarks, old cells which in their attempts at secretion under the new circumstances of active need of milk,

* Fig. 402. Globules and molecules of cow's milk $\frac{400}{1}$.

are filled with oily matter; which, however, being unable to discharge, they are themselves shed bodily to make room for their successors. Colostrum-corpuscles have been seen to exhibit contractile movements and to squeeze out drops of oil from their interior (Stricker).

Chemical Constitution of Milk.

Milk is in reality an emulsion consisting of numberless little globules of fat, coated with a thin layer of albuminous matter, floating in a large quantity of water, which contains in solution albumin, milk-sugar (lactose), and several salts. Its percentage composition has been already mentioned (p. 275). Its reaction is always alkaline: its specific gravity about 1030.

When milk is allowed to stand, the fat globules, being the lightest portion, rise to the top, forming *cream*.

If a little acetic acid be added to a drop of milk under the microscope, the albuminous film coating the oil drops is dissolved, and they run together into larger drops. The same result is produced by the process of *churning*, the effect of which is to break up the albuminous coating of the oil drops: they then coalesce to form *butter*.

If milk be allowed to stand for some time, its reaction becomes acid: in popular language it "turns sour." This change appears to be due to the conversion of the milk-sugar into lactic acid, which causes the precipitation of the casein (curdling): the curd contains the fat globules: the remaining fluid (whey) consists of water holding in solution milk-sugar and certain salts. The same effect is produced in the manufacture of cheese, which is really casein coagulated by the agency of rennet (p. 37). When milk is boiled, a scum of casein forms on the surface; this is rapidly succeeded by a second if the first be removed.

The salts of milk are chlorides, sulphates, phosphates, and carbonates of potassium, sodium, calcium.

APPENDIX.

MEASURES OF WEIGHT (*Avoirdupois*).

(*Averages.*)

		lbs.	ozs.
Recent Skeleton		21	8
Muscles and Tendons		77	8
Skin and Subcutaneous tissue		16	5
Blood		11 to 14	–
Brain	Cerebrum	2	12
	Cerebellum	–	5¼
	Pons and Medulla oblongata	–	1
	Encephalon	3	2¼
Eyes		–	½
Heart		–	10
Intestines, small		1	11½
,, large		1	1
Kidneys (both)		–	10½
Larynx, Trachea, and larger Bronchi		–	2¾

		lbs.	ozs.
Liver		3	8
Lungs (both)		2	10
Œsophagus		–	1¾
Ovaries (both)	¼ to	–	½
Pancreas		–	3
Salivary Glands (both sides),	1½ to	–	2
Stomach		–	7
Spinal Cord, divested of its nerves and membranes		–	1½
Spleen		–	7
Suprarenal Capsules (both),	⅛ to	–	¼
Testicles (both)	1½ to	–	2
Thyroid body and remains of Thymus gland		–	¾
Tongue and Hyoid bone		–	3
Uterus (virgin)	⅓ to	–	¾

MEASURES OF LENGTH. (*Average.*)

		ft.	in.
Appendix vermiformis	3 to	–	6
Bronchus, right		–	1½
,, left		–	2½
Cæcum		–	2½
Duct, common bile		–	3
,, ,, ejaculatory,	¾ to	–	1
,, of Cowper's gland		–	1¼
,, hepatic		–	2
,, nasal		–	¾
,, parotid		–	2½
,, sub-maxillary		–	2
Epididymis		–	1¾
,, unravelled		20	–
Eustachian tube		–	1½
Fallopian tube		–	3½
Intestine, large	5 to	6	–
,, small		20	–

		ft.	in.
Ligament, round, of uterus		–	4½
,, of ovary		–	1½
Meatus auditorius externus		–	1¼
Medulla oblongata		–	1¼
Œsophagus		–	10
Pharynx		–	4½
Rectum		–	8
Spinal cord		1	5
Tubulus seminiferus		2	3
Urethra, male		–	8
,, female		–	1½
Ureter		1	4
Vagina	4 to	–	6
Vas deferens		2	–
Vesicula seminalis		–	2
,, ,, unravelled,	4 to	–	6
Vocal cord		–	½

SIZES OF VARIOUS HISTOLOGICAL ELEMENTS AND TISSUES.

(Average size in fractions of an inch.

Air-cells, $\frac{1}{70}$ to $\frac{1}{30}$.
Blood-cells (red), $\frac{1}{3200}$ (breadth).
" " $\frac{1}{10000}$ (thickness).
" (colourless), $\frac{1}{2500}$.
Canaliculus of bone, $\frac{1}{7000}$ (width).
Capillary bloodvessels, $\frac{1}{3000}$ (lung) to $\frac{1}{1500}$ (bone).
Cartilage-cells (nuclei of), $\frac{1}{3000}$.
Chyle-molecules, $\frac{1}{30000}$.
Cilia, $\frac{1}{5000}$ to $\frac{1}{2500}$ (length).
Cones of retina (at yellow spot), $\frac{1}{12000}$ to $\frac{1}{10000}$ (width).
Connective-tissue fibrils, $\frac{1}{50000}$ to $\frac{1}{15000}$ (width).
Dentine-tubules, $\frac{1}{4500}$ (width).
Enamel-fibres, $\frac{1}{5000}$ (width).
End-bulbs, $\frac{1}{300}$.
Epithelium
columnar (intestine), $\frac{1}{2000}$ (length).
spheroidal (hepatic), $\frac{1}{1000}$ to $\frac{1}{500}$.
squamous (peritoneum), $\frac{1}{1000}$ (width).
" (mouth), $\frac{1}{500}$ "
" (skin), $\frac{1}{300}$ "
Elastic (yel.) fibres, $\frac{1}{24000}$ to $\frac{1}{4000}$ (wide).
Fat-cells, $\frac{1}{500}$ to $\frac{1}{400}$.
Germinal vesicle, $\frac{1}{720}$.
" spot, $\frac{1}{3000}$.
Glands
gastric, $\frac{1}{30}$ to $\frac{1}{20}$ (length).
" $\frac{1}{500}$ to $\frac{1}{350}$ (width).
Lieberkuhn's (small intestine), $\frac{1}{350}$ to $\frac{1}{250}$ (length).
Lieberkuhn's (small intestine), $\frac{1}{500}$ (width).
Peyer's (follicles), $\frac{1}{24}$ to $\frac{1}{12}$.
sweat, $\frac{1}{70}$ (width).
" in axilla, $\frac{1}{36}$ to $\frac{1}{8}$ (width).

Haversian canals, $\frac{1}{1000}$ to $\frac{1}{200}$ (width).
Lacunæ (bone), $\frac{1}{1800}$ (length).
" " $\frac{1}{3600}$ (width).
Macula lutea, $\frac{1}{24}$.
Malpighian bodies (kidney), $\frac{1}{120}$.
" corpuscles (spleen), $\frac{1}{60}$ to $\frac{1}{30}$.
Muscle (striated), $\frac{1}{500}$ to $\frac{1}{400}$ (width).
" -cell (plain), $\frac{1}{600}$ to $\frac{1}{300}$ (length).
" " " $\frac{1}{4500}$ to $\frac{1}{3500}$ (width).
Nerve-corpuscles (brain) $\frac{1}{3000}$ to $\frac{1}{300}$.
" -fibres (medullated) $\frac{1}{12000}$ to $\frac{1}{1500}$ (width).
" " (non-medullated) $\frac{1}{3000}$ to $\frac{1}{5000}$ (width).
Ovum, $\frac{1}{120}$.
Pacinian bodies, $\frac{1}{15}$ to $\frac{1}{10}$ (length).
" " $\frac{1}{25}$ to $\frac{1}{20}$ (width).
Papillæ of skin (palm), $\frac{1}{400}$ to $\frac{1}{150}$ (length).
" " (face), $\frac{1}{500}$ to $\frac{1}{300}$ "
" tongue (circumvallate), $\frac{1}{20}$ to $\frac{1}{12}$ (width).
" " (fungiform), $\frac{1}{35}$ to $\frac{1}{25}$ (width).
" " (filiform), $\frac{1}{10}$ (length).
Pigment-cells of choroid (hexagonal), $\frac{1}{1000}$.
" granules, $\frac{1}{20000}$.
Spermatozoon, $\frac{1}{600}$ to $\frac{1}{500}$ (length).
" head, $\frac{1}{5000}$ "
" " $\frac{1}{10000}$ (width).
Touch-corpuscle, $\frac{1}{300}$ (length).
Tubuli seminiferi, $\frac{1}{200}$ to $\frac{1}{100}$ (width).
" uriniferi, $\frac{1}{500}$.
Villi, $\frac{1}{50}$ to $\frac{1}{8}$ (length).
" $\frac{1}{250}$ to $\frac{1}{70}$ (width).

METRICAL SYSTEM OF WEIGHTS AND MEASURES COMPARED WITH THE COMMON MEASURES.

Metre . .	=	$39\frac{3}{8}$ inches (about).	Gramme .	=	$15\frac{1}{2}$ grains (nearly).
Centimetre .	=	$\frac{2}{5}$ inch (nearly).	Centigramme .	=	$\frac{3}{20}$ grain (about).
Millimetre .	=	$\frac{1}{25}$ " "	Milligramme .	=	$\frac{3}{200}$ " "

SPECIFIC GRAVITY OF VARIOUS FLUIDS AND TISSUES.

(*Water* = 1·000).

Adipose tissue	0·932	Liver	1·055
Bile	1·020	Lymph	1·020
Blood	1·055	Lungs	
,, corpuscles (red)	1·088	when fully distended	0·126
Body (entire)	1·065	ordinary condition, post mortem	0·345 to 0·746
Bone	1·870 to 1·970	when deprived of air	1·056
Brain	1·036	Muscle	1·020
,, grey matter	1·034	Milk	1·030
,, white	1·040	Pancreatic juice	1·012
Cartilage	1.150	Saliva	1·006
Cerebro-spinal fluid	1.006	Serum	1·026
Chyle	1·024	Spleen	1·060
Gastric juice	1.0023	Sweat	1·004
Intestinal juice	1·011	Urine	1·020
Kidney	1·052		
Liquor amnii	1·008		

TABLE SHOWING THE PERCENTAGE COMPOSITION OF VARIOUS ARTICLES OF FOOD. (Letheby.)

	Water.	Albumen.	Starch.	Sugar.	Fat.	Salts.
Bread	37	8·1	47·4	3·6	1·6	2·3
Oatmeal	15	12·6	58·4	5·4	5·6	3·
Indian corn meal	14	11·1	64·7	0·4	8·1	1·7
Rice	13	6·3	79·1	0·4	0·7	0·5
Arrowroot	18	–	82·	–	–	–
Potatoes	75	2·1	18·8	3·2	0·2	0·7
Carrots	83	1·3	8·4	6·1	0·2	1·0
Turnips	91	1·2	5·1	2·1	–	0·6
Sugar	5	–	–	95·0	–	–
Treacle	23	–	–	77·0	–	–
Milk	86	4·1	–	5·2	3·9	0·8
Cream	66	2·7	–	2·8	26·7	1·8
Cheddar cheese	36	28·4	–	–	31·1	4·5
Lean beef	72	19·3	–	–	3·6	5·1
Fat beef	51	14·8	–	–	29·8	4·4
Lean mutton	72	18·3	–	–	4·9	4·8
Fat mutton	53	12·4	–	–	31·1	3·5
Veal	63	16·5	–	–	15·8	4·7
Fat pork	39	9·8	–	–	48·9	2·3
Poultry	74	21·0	–	–	3·8	1·2
White fish	78	18·1	–	–	2·9	1·0
Eels	75	9·9	–	–	13·8	1·3
Salmon	77	16·1	–	–	5·5	1·4
White of egg	78	20·4	–	–	–	1·6
Yelk of egg	52	16·0	–	–	30·7	1·3
Butter and fats	15	–	–	–	83·0	2·0
Beer and porter	91	0·1	–	8·7	–	0·2

CLASSIFICATION OF THE ANIMAL KINGDOM.

VERTEBRATA.

	Typical Examples.
Mammalia	
Primates	Man.
"	Ape, baboon.
Chiroptera	Bat, flying fox.
Insectivora	Mole, hedgehog.
Carnivora	Lion, dog, bear, seal.
Proboscidea	Elephant.
Hyracoidea	Hyrax.
Ungulata:	
Perissodactyla	Tapir, rhinoceros, horse.
Artiodactyla	Hippopotamus, pig, camel, chevrotain, deer, ox, sheep, goat, giraffe.
Sirenia	Dugong, manatee.
Cetacea	Whale, porpoise, narwhal.
Rodentia	Hare, porcupine, guinea pig, rat, beaver, squirrel, dormouse.
Edentata	Armadillo, pangolin, true anteater, Cape anteater, sloth.
Marsupiata	Opossum, bandicoot, Thylacinus, phalanger, wombat, kangaroo.
Monotremata	Ornithorhynchus or duck-billed platypus, Echidna or spiny anteater.
Birds	
Carinatæ	
Raptores (*Birds of prey*)	Vulture, hawk, owl.
Scansores (*Climbing Birds*)	Woodpecker, parrot.
Passeres (*Perching Birds*)	Crow, finch, swallow.
Rasores (*Scratching Birds*)	Fowl, pheasant, grouse.
Grallatores (*Wading Birds*)	Heron, stork, snipe, crane.
Natatores (*Swimming Birds*)	Penguin, duck, pelican, gull.
Ratitæ	
Cursores (*Running Birds*)	Ostrich, emeu, apteryx.
Reptiles	
Crocodilia	Crocodile, alligator.
Lacertilia	Iguana, chameleon, gecko, lizard, slowworm, flying dragon.
Chelonia	Tortoise, turtle.
Ophidia	Snake, viper.
Amphibia	
Anura	Frog, toad.
Urodela	Newt, salamander.
Fish	
Dipnoi	Lepidosiren.
Teleostei	Perch, mackerel, cod, herring.
Placoidei	Shark, ray.
Ganoidei	Sturgeon, bony pike.
Cyclostomi	Lamprey, hag.
Leptocardii	Amphioxus lanceolatus.

CLASSIFICATION OF THE ANIMAL KINGDOM.

INVERTEBRATA.

	Typical Examples.
Mollusca	
Cephalopoda	Octopus, argonaut, squid, cuttle-fish, nautilus.
Pteropoda	Clio, Cleodora.
Gasteropoda:	
Pulmonigasteropoda	Snail, slug.
Branchiogasteropoda	Whelk, limpet, periwinkle.
Lamellibranchiata	Oyster, mussel, cockle.
Brachiopoda	Terebratula, Lingula.
Tunicata, or Ascidioidea	Salpa, Pyrosoma.
Bryozoa or Polyzoa	Sea mat.
Arthropoda	
Insecta	Beetle, bee, ant, locust, grasshopper, cockroach, earwig, moth, butterfly, fly, flea, bug.
Arachnida	Scorpion, spider, mite.
Myriopoda	Centipede, millipede.
Crustacea	Crab, lobster, cray-fish, prawn, barnacle.

Annulata	Sea-mouse, leech, earthworm.
Scolecida	Hair-worm, thread-worm, round-worm, fluke, tape-worm, guinea-worm.
Echinodermata	Sea-cucumber, sea-urchin, star-fish, sand-star, feather-star.
Cœlenterata	
Ctenophora	Beroe.
Anthozoa	Sea anemone, coral, sea-pen.
Hydrozoa	Hydra, Sertularia, Velella, Portuguese man-of-war.
Spongida	Sponges.
Protozoa	
Rhizopoda	Foraminifera, Amœba.
Infusoria	Paramœcium, Vorticella.

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